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From the German of the late

...N KERNER VON MARILAUN

By

F. W. OLIVER, M.A., D.Sc.

With the Assistance of

...SK. B.Sc. and MRS. M. F. MACDONALD, B.Sc.

Two Thousand Original Woodcut Illustrations

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The Natural History of Plants

Their Forms, Growth, Reproduction, and Distribution

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THE

NATURAL HISTORY OF PLANTS.

INTRODUCTION.

Sources of a History of Plants. — The Language of Botanists.

SOURCES OF A HISTORY OF PLANTS.

FROM the sixteenth to the latter part of the eighteenth century, "Historia plantarum" was the customary title for botanical works. Most of the scholars of that time took as their authorities and models the writings of Theophrastus, the celebrated pupil of Aristotle, together with the thirty-seven books constituting Pliny's "Historia naturalis". Thus it came about that the titles of the new books were similar to those of Theophrastus and Pliny. However, all these books are anything but histories of plants, if in the idea of a history we include an account of the changes which occur within the limits of space and time. In reality the bulky folios of Clusius, Bauhin, and Haller, the title-pages of which bear the inscription "Historia plantarum", contain descriptions merely of the external characters of plants, accompanied by only sparing details of the situations in which these plants had been found growing wild. Works of this kind, dealing with limited areas of country, were later on distinguished by the name of Floras. By this name they are still known.

Although the authors of the Flora had no such purpose in view, their works furnished the starting-point for a real history of the vegetable world. A comparison of the Floras of neighbouring regions shows that certain plants inhabit a greater, others a lesser area; that the boundaries of the species confined to a distinct district coincide with territories inhabited by various races of mankind; that the boundaries of this and that species coincide and stand in relation to various climatic and other conditions.

All plants have the power of propagating themselves. They send their offspring forth as colonists towards all points of the compass, and endeavour in this way to enlarge their areas of distribution. Suppose that a species hitherto subsisting in localities where there are seven months of snow and five months of vegetation in the year multiplies, and that its descendants are scattered in all directions, what would happen if any of these emissaries reached places where frost and snow

prevail for eight months instead of seven, and where the season for vegetation is confined to four months? They would succumb to the inhospitality of the climate; and it follows that a limit to the distribution of the species in question would be attained at a line connecting all places which possess a climate of equal rigour. This does not preclude the possibility of other causes constituting a barrier to the distribution of the same species in other directions. Peculiarities of soil, for instance, may prevent the naturalization of a plant; or, its spread may be baffled by the opposition of plants already long settled in the place invaded; or any other like impediment may operate as a check. Facts of this kind, being brought to light by the comparison of different Floras, led to detailed research into the means of reproduction and distribution in plants, to a study of the many contrivances for their propagation, and of the nature of the equipments which enable the descendants of a stock to enlarge the area where it grows.

Side by side with these investigations into the history of individual kinds of plants, there was developed a special department of research with the view of determining the actually-existing boundary-lines of distribution — the so-called lines of vegetation—of particular species, and of ascertaining all the conditions of soil and climate affecting plant-life which prevail along these lines, so as to take into consideration all the possible causes of limits to distribution. The range of observations was likewise extended to displacements of the lines of vegetation, to the advance of particular species in one direction or another, and the suppression and annihilation of others within historic times; thus a chronicle of plant migration was started.

The unlooked-for discovery of the multitude of plants which flourished upon the earth ages ago, and have been preserved as fossils, led to a further comparison of forms—viz. of those now living with those that have perished. There was no evading the idea that existing species are derived from others now extinct; on the contrary it proved so attractive that it was followed up with the greatest interest and zeal. Then these inquiries into the parentage of species naturally led further to the whole problem of their origin—in short, to a study of the history of species.

The range of vision continued to become yet wider. It is impossible that the dwarf willows and birches found living in Greenland at the present day should be descendants of the maples and beeches which grew there in the Tertiary Period, or that the alders or pines now flourishing on the soil above the beds of bituminous coal at Häring in Tyrol should have sprung from the Proteaceæ and Myrtaceæ which formerly covered the same ground, as we learn from the fossil remains found there. Local changes must have taken place, and the various floras must have undergone a process of expatriation on a large scale not unlike that of men at the time of the migration of tribes. New realms were then occupied by those floras in a manner corresponding to the formation of states by the struggling and mingling races and nations of mankind. The knowledge of the fact that a plant's form depends at the present day upon soil and climate entitles us, moreover, to infer that a similar connection existed in past times between the forms of plants and their

conditions of life, and enables us to discover what gave rise to migrations and caused the redistribution of floras. These phenomena are the subject-matter of the History of the Plant World in the fullest meaning of the phrase; and their explanation is eagerly sought by modern botanists.

In 1853 Unger, to whom all branches of Botany were equally familiar, made the first attempt at such a history of plants. Since then a great number of new discoveries have been made both in the Old World and the New. Men with minds intent upon this object are everywhere searching for the fossil remains which throw such valuable light upon it; but, so far, this—the most recent branch of Botany—has not led to a comprehensive result. We find ourselves, as it were, in the midst of a stream in full flood owing to the number and magnitude of its tributaries, and it is no easy matter to steer clear of shoals and run safely into harbour. Some decades hence it may perhaps be possible to write an accurate and complete history of the plant world founded upon the mass of authentic evidence which will by that time have been winnowed from the records of past ages. At present I must content myself with sketching in general, and often ill-defined, outline the changes which take place in the world of plants.

The foregoing introductory remarks concerning the sources from which materials for a history of plants are derived serve also to explain the arrangement of the subject-matter to be dealt with in the Second Volume of this work. The order of presentation of the different parts of the subject will follow the stages of development of the science. A history of the entire plant-world considered as a single great community must be preceded by a history of species. But each species is the sum of numberless individuals, which are alike in constitution and have the same external characteristics, and a history of species therefore presupposes a knowledge of the history of the individual. Accordingly, our first business is to describe the rejuvenescence, multiplication, and distribution of individuals, and to show by what means a plant, considered as a separate organism, maintains itself, takes possession of its habitat, and is enabled to keep its hold on that habitat up to the moment when it is replaced by descendants endowed with a vitality of their own.

THE LANGUAGE OF BOTANISTS.

Before entering upon a description of any of the above phenomena, I feel it necessary to say a few words respecting the technical botanical terms of which I shall make use. The need of short and compendious names to denote particular forms, particular organs, and particular processes, has been always universally recognized, and more or less appropriate additions to our vocabulary have been made by men of science from time to time. As might be expected, these designations are not only an expression of the particular standpoint to which, at the time of their invention, the actual knowledge of plant-life had most recently attained; but they are also liable to bear the stamp of theories advanced by eminent

naturalists of the day, or of the hypotheses which happened to be then in vogue. The progress of true knowledge is too often hindered by the fact that men exalt their speculative theories to the position of "laws of nature", and when they first encounter contradictory evidence twist and turn it until it appears actually to verify those theories. We need not inquire in these instances how much is due to self-deception and how much to prejudice and dogmatism on the part of the investigators. Certain it is that such a perverse method of research, especially when supported by the authorized beliefs of the thoughtless multitude, acts as a drag on true science. Fortunately, however, it is nothing worse than a drag. For, sooner or later, the conviction again asserts itself that our notions respecting the history of plants must be derived from the facts observed in their entirety and purity, instead of facts being made to fit a preconceived opinion—some being explained away as exceptions, whilst others are altogether ignored and suppressed.

In all sciences for which it is requisite to invent technical terms—and in Botany no less than in others—we find that the terminology bears traces of ideas formed at earlier periods, and now rejected as being based on insufficient experiment or imperfect observation, on self-deception or prejudice, as the case may be. The question has, therefore, repeatedly been raised whether it is better to retain such names and modes of expression, although they are likely to suggest wrong ideas to students, or to abolish them and substitute new ones in their stead. There are strong arguments for both courses. The chief advantage of retaining the old terms is that readers of modern works are thereby enabled to understand more easily the writings of older botanists. We have also to consider the probability that in rejecting old terms and inventing new ones we may fall into the same errors as our predecessors. Any one who has worked in the field of Botany for more than forty years, as I have done, must have found that on an average every ten years prevailing ideas have undergone a change. He has seen how theories, which for a time influenced every branch of the science, and were actually standard conceptions in many departments of research, have sooner or later had to give place to new ones. He knows how often a naturalist is compelled, in consequence of fresh and unexpected discoveries, to let go a position which he has considered impregnable, and which has become endeared to him by long familiarity. Thus, experience teaches diffidence, and one learns to attribute only a temporary value, so to speak, even to one's own original theories, and to rest assured that, in a few decades, what now appears to be nearest the truth will be superseded by something else which comes still nearer to it.

But if, whenever a fresh stage of knowledge were reached, all terms and phrases which had become antiquated and no longer quite applicable were abandoned and replaced by others, and if in addition new names were introduced corresponding to every modification in the results obtained by observing all the different processes and appearances with which we have to deal, our science would inevitably be rendered far less accessible—and this consequence would be much to

be regretted. However strong the desire to understand the secrets of plant-life, it could only be satisfied at the cost of learning a special scientific language; and Botany would become, in an even greater degree than is the case at present, a close study for specialists, instead of being the common property of the many inquiring minds to whom the results of our researches by right belong.

Accordingly, we shall retain so far as is practicable the recognized scientific terms. Where they are no longer quite suitable they will be briefly elucidated; and, when the conceptions to which they refer have been expanded or limited, the old established names will also be taken in a wider or a narrower sense as the case may be. New expressions will only be introduced where their use is productive of greater clearness and distinctness in the ideas involved; and even these additions must be in harmony with the terms already in existence.

It is worthy of note too that many foreign words, which have been longest established and also subject to frequent use by botanists, originally meant something altogether different from what they are intended to denote at the present day. In the very first section of this volume a whole series of such words will be employed. The history of the plant-individual is there dealt with. What is an "individual"? The word comes from *dividere*, to divide, and denoted originally a thing which is not divisible. But there is no such thing as an indivisible plant. The survival of plants, their reproduction and multiplication, are all dependent on processes of division; and any species whose individuals were not divisible, would be doomed to inevitable destruction. The characteristic property of an individual cannot therefore lie in absolute indivisibility. A qualification has in consequence been inserted in the definition, and an individual is explained to be a thing which cannot be divided without ceasing to be, as heretofore, an organized being subsisting independently, in which each single part belong indispensably to the whole. Even this definition is not appropriate to a plant. The living protoplast of a unicellular plant—an organism which must without question be conceived as an individual—divides into two halves, which separate from one another and constitute two independent individuals. This instance affords, however, an indication of the true definition. A plant-individual is an organism which can and does live independently and without the aid of other organisms of the same form. There are plant-individuals each of which consists of a single protoplast, whilst others are composed of many protoplasts living together. In the latter there is for the most part a division of labour accompanied by a corresponding variety in the forms of the different parts of the individual; but even in these cases individuality is not necessarily destroyed by division. Where division of labour has been carried so far as it is in a plant provided with stem and leaves (*cf.* vol. i. p. 584), it used to be thought necessary to look upon the structure as an association of individuals. Each single shoot was conceived to be an individual because it possessed the power of continuing to live after it had been separated from the axis, and on that assumption each one of the higher plants was built up of such and such a number of separate individuals. Later on, however, inasmuch as every branch of a shoot

is capable of living when separated from the rest and of producing a new independent plant, the parts of a shoot came to be considered as being individuals, and the term "Anaphytes" was applied to them. We shall see hereafter the extent to which this conception is of importance in relation to the subject of alternation of generations. It would be out of place to treat it more fully at present.

Another conception of the plant-individual must also be mentioned here. When the impossibility of defining it as indivisible was recognized, the strange expedient was invented of assuming the existence of divisible individuals and of representing all parts which have been produced asexually and have become independent as belonging to a single individual. A potato puts forth thirty or forty fresh tubers in the course of a few years, and all these were considered as collectively constituting one single individual, as also were the countless young carnation-plants which are to be derived by means of cuttings from one old plant. The general rule was that only an organism produced by sexual process was to pass as an individual. Cuttings, tubers, and the like, detached from such an organism would be, according to this conception, merely parts of one individual, even though they were capable of living quite independently and at a distance from one another.

This definition, the invention of philosophers, has never been taken seriously by naturalists, and I only cite it because it introduces another important problem which I purpose to treat in an exhaustive manner in the first three sections of this volume, namely, the question of the propagation or generation of plants. The modes of reproduction in plants have been subjected in recent times to most patient investigation on the part of botanists gifted with the keenest powers of observation, and their researches have led to the conclusion that in most—probably in all—divisions of the vegetable kingdom two kinds of propagation occur. In each case a single protoplast forms the starting-point for the new individual; but, in the one, this protoplast does not require the special stimulus afforded by union with another protoplast, whereas, in the other, in order that a new individual organism may be produced, a pairing—*i.e.* a union of the substances—of two protoplasts, which have come into being at different spots, must take place. The former is called *asexual* reproduction, the latter *sexual* reproduction. All reproductive bodies arising asexually are included under the name of *brood-bodies*, whilst those which are associated with the sexual process may be termed broadly *fruits*.

There are all grades of brood-bodies, from the single cell to the completely formed plant. Brood-bodies, if unicellular, are termed *spores*, if multicellular, *thallidia*; and those which constitute rudimentary shoots are called *buds*. The bud form of brood-body either detaches itself from the living parent-plant, or else, as more frequently happens, it becomes independent through the death of the plant from which it sprang. In the latter case the off-shoots remain in the immediate vicinity of the parent-plant. In the case of trees and shrubs the buds do not sever themselves from the axis on which they were developed, but continue their connection with it as they grow into shoots, and in this manner are formed those compound individuals to which reference has been already made. It is much less

common for full-grown shoots to detach themselves from the parent-plant and act as brood-bodies.

Fruits of all degrees of complexity are also found. They are sometimes single cells, sometimes groups of cells, and sometimes complete plants in miniature. Usually the fruit—or at least the most important part of it which contains the fertilized ovum or the embryo produced thereby—becomes detached, when ripe, from the parent-plant; but, in many groups of the vegetable kingdom, in Ferns, Mosses, Lichens, and Florideæ, for example, the fruit remains at its place of origin and preserves its connection with the mother-plant whilst itself developing into a new generation, which, however, does not produce fruits but spores. When asexual and sexual reproduction take place alternately in a definite manner, we speak of an *Alternation of Generations*. Hitherto the subjects of fruit-formation and of the alternation of generations in their relation to the History of Plants have remained unrecognized and unelucidated. In one of the following sections of this volume an attempt will be made to solve this great mystery.

THE GENESIS OF PLANT-OFFSPRING.

1. ASEXUAL REPRODUCTION.

Spores and Thallidia.—Buds on Roots.—Buds on Stems.—Buds on Leaves.

SPORES AND THALLIDIA.

In the chapters on ferns in the old herbals, attention is invariably directed to the extraordinary phenomenon that the plants in question do not produce flowers or fruit, and yet propagate their kind and multiply abundantly, and the remark is made that these plants will often spring up quite unexpectedly in caves, or in the cracks of old walls, without any seeds having been previously perceptible there. Hence in Germany a fabulous story was invented that the seeds of ferns were formed in a mysterious manner at the time of the summer solstice only, and that these seeds could only be collected on Midsummer Eve by persons initiated in the mystery who made use of certain magic words on the occasion. Hieronymus Bock or Tragus, as he called himself in accordance with the then prevailing fashion of translating names into Greek, preacher and physician at Hornbach in 1532, was the first to contradict this childish superstition, and to convince himself of the possibility of obtaining "fern-seeds" without the use of incantations. In his Herbal, published in 1539, he gives the following account, which is in many respects interesting, of his endeavours to collect the seeds of ferns: "All our teachers write that the fern bears neither flower nor seed; nevertheless, I have four times looked for the seed in the night of Midsummer Eve, and have found early in the morning before daybreak small black seeds like poppy-seeds on cloths and on the broad leaves of mullein beneath the stems in varying quantities. . . . I have used no charm or spell in this matter, but have looked for the seeds without any superstition and have found them. One year, however, I found more than another, and I have sometimes been out without success. I have not gone alone to fetch the seeds, but have taken two others with me, and have made a great fire in an unfrequented spot and let it burn all through the night. How the thing came to pass, and what secret nature intends to reveal by it, I cannot tell. I have stated all this because all our teachers describe the fern as being without seeds."

There can be no doubt that by the brown seeds Hieronymus Bock meant those structures which, about two centuries later, were named "spores" by Linnæus. But even in the time of Linnæus the whole subject of spores, especially in their relation to fruit, was shrouded in complete obscurity. The word "spore" is derived from

the Greek, and signifies etymologically precisely the same as "seed", and spores were considered to be peculiar seeds, formed by means of some mysterious processes of fructification. As late as fifty years ago the spore was defined as "that part of a cryptogamic plant which corresponds to the seed, and from which, although it contains no germ, a new plant can be developed".

The mode of fructification in the Fern, and, in general, the entire history of its development, were discovered for the first time in 1848. It was then shown that these plants pass through two kinds of regularly alternating generations. One of these is itself inconspicuous, but bears reproductive organs and produces fruits; the other, springing from the fruit, which continues its connection with the parent-plant, is distinguished by fronds and produces spores. Thus the fronds of Ferns bear no sexual reproductive organs, and the spores formed upon them cannot therefore be looked upon as fruits or even as seeds, a seed being part of a fruit.

Some people, it is true, treat the entire frond-bearing Fern-plant as a fruit and the spores on the fronds as part of this fruit, although such a theory involves the admission that fruits may strike root, multiply by means of runners and continue to grow for many years, putting forth annually new spore-bearing fronds. According to this view, which I cannot endorse, a gigantic tree-fern, aged a hundred years, would be a fruit, and to be consistent it would be necessary to regard a whole grove of Horse-tails as belonging to one single fruit. Other botanists, whilst denying that the Fern-plant with its roots and fronds is the fruit itself, are yet of opinion that the formation of spores in the Fern is a consequence of the process of fruiting, inasmuch as the Fern-plant would never make its appearance at all but for the formation of fruit by the previous generation; and they hold that the spores of Ferns, and of their allies the Horse-tails and Club-mosses, should on that account be distinguished from those of other Cryptogams. To this view there are two objections. In the first place, we know many cases wherein a Fern-plant with spore-bearing fronds is developed from the first generation without any formation of fruit having taken place, and the plant in these instances is in no way different from those which have sprung from fruits of the first generation. Secondly, it is difficult to see why the sporogenous generation should be more dependent on the fruit of the first generation in the case of Ferns than in many other Cryptogams, which similarly exhibit an alternation of generations.

As the spores of Ferns, and of Cryptogams in general, are not the direct result of a process of fertilization, they are not parts of fruit, but are brood-bodies. They should be placed by the side of the bud forms of brood-body presently to be described, though differing from these in that they always produce a single layer (*i.e.* a thallus) only, and never a leafy, axial structure. They are just as characteristic of Cryptogams as buds are of Phanerogams or Flowering Plants, and as the name of Cryptogam is no longer quite appropriate, it is often replaced by the term "sporogenous plant". Before the discovery of the alternation of generations in Cryptogams, the name spore was applied to many fruits and rudiments of fruits, particularly where these happened to be unicellular, an error which we should be

careful to avoid at the present day. When we come to the description of fruits and their origin, we shall have occasion to return again to this subject.

The places where spores originate are remarkably varied. In some plants nests of cells make their appearance in the interior of an extensive tissue; in others single cells are exposed on the surface. The task of spore-development devolves sometimes upon a part of a green stem or leaflet. Sometimes—in plants devoid of chlorophyll—upon the protoplasmic contents of a tubular structure, and sometimes upon the abstricted ends of hyphal filaments. The best way to arrive at an idea of the extreme diversity in this respect is to classify spores in groups according to their mode of origin. (Cf. p. 20.)

One group comprises all such spores as are formed in the cells of a tissue. Amongst these are the spores of Ferns, Rhizocarps, Horse-tails, Club-mosses, and the numerous kinds of Mosses and Liverworts. In one sub-group of Ferns papillæ spring singly from the epidermis clothing the ribs of the fronds, each papilla being divided by a transverse wall into a free extremity and a stalk-cell. Both cells of the papilla become partitioned so as to form bodies of tissue, and the one that developes from the free terminal cell assumes an oval or spherical shape. In this latter ball of tissue a tetrahedral central cell and an envelope composed of several layers of cells may be distinguished. By internal partition of the central cell a little cluster of cells is formed, whilst, in the meantime, the inner layer of cells composing the envelope is dissolved, so that the whole now assumes the aspect of a receptacle inclosing a ball of cells embedded in a fluid matrix. Each cell of the cluster next divides into four compartments, and the protoplasts which constitute the contents of these chambers provide themselves with membranes and become disconnected upon the solution of the framework of their home. These separated cells are the spores. To the naked eye they have the appearance of a powdery mass. As has been said, of the cell-layers which formed the envelope of the sporogenous tissue, only the inner one was dissolved; the outer layer persists and constitutes a kind of capsule, to which the name of spore-case or "sporangium" is applied (see figs. 189[13], 189[14], 189[15]). A collection of sporangia of this sort is called a "sorus". In the Polypodiaceæ—a family of Ferns to which the majority of European species belong—the sori may be seen on the backs of the fronds (see 189[5]). Upon the veins running through the green tissue are seated little cushion-like groups of cells. Each cell in one of these cushions is capable of developing into a stalked sporangium, and sometimes a single sorus consists of no less than fifty such stalked sporangia. In the Cyatheaceæ also, which include most of the Tree-ferns, the sori are developed on the under side of the fronds, but in their case each is borne on a kind of peg projecting at right angles to the surface of the frond. The sporangia derived from the epidermal cells of this peg are very shortly stalked. An annular wall is produced from the green tissue of the frond and surrounds the sporangiferous peg, which consequently stands up from the middle of a cup (see figs. 189[10], 189[11], 189[12]).

In the delicate and graceful Hymenophyllaceæ—Ferns with a resemblance to

Fig. 189.—Ferns.

Nephrolepis Duft. [2] *Trichomanes Lyelli.* [3] Sorus of the same Fern with cup-shaped investment seen in longitudinal section. [4] *Rhipidopteris peltata.* [5] *Polypodium serpens.* [6] Pinna of *Gleichenia alpina.* [7] *Schizæa fistulosa.* [8] *Botrychium lanceolatum.* [9] Under side of a pinna of *Gleichenia alpina*; in the two upper cavities the sporangia are covered by leaflets, in the under ones they are exposed. [10, 11] Pinna of *Cyathea elegans.* [12] Longitudinal section through a Sorus and Cup of *Cyathea.* [13] Sporangium of *Cyathea.* [14] Sporangium of *Polypodium.* [15] Sporangium of *Schizæa.* [16] Under side of the Frondallium of Spleenwort. [1, 2, 4, 5, 6, 7, 8] natural size; [3, 9, 10, 11, 12, 13, 14, 15, 16] magnified from 5 to 20 times.

Mosses, and belonging for the most part to tropical regions—the veins of the pinnæ project beyond the margin of the green tissue and form styloid processes whose epidermal cells become the points of origin of sporangia. Each styloid process thus constitutes an axis bearing the sporangia, and the entire sorus has the form of a little spike. But the sorus itself stands in a cup formed by an upgrowth of the green tissue at the margin of the pinna (see figs. 189[2] and 189[3]).

In the three groups of Ferns above dealt with the sporangia arise from epidermal cells. In the Gleicheniaceæ and Schizæaceæ (two specimens of which are shown in figs. 189[6] and 189[7]) the sporangia are modified leaflets. We must here remark that the fronds of Ferns in spite of their similarity to foliage-leaves are not to be regarded as such, but as phylloclades, whilst the scales upon the fronds must be considered to be leaves. We shall refer to this again later on. Now, in Gleicheniaceæ and Schizæaceæ some of these small scaly leaves are metamorphosed into sporangia which here take the form of rounded bodies set in rows of pit-like cavities hollowed out of the pinnæ, whilst other scales constitute protective coverings to these sporangia. The relation existing between the various parts in the case of a pinna of *Gleichenia alpina* is shown very clearly on an enlarged scale in fig. 189[9].

In respect of origin and development the spores and sporangia are again quite different in the group of Ferns comprised under the name of Ophioglosseæ, one species of which—viz. the spear-shaped Moonwort (*Botrychium lanceolatum*)—is represented in fig. 189[8]. In these Ferns, the sporogenous portions take the form of nests of cells embedded in the tissue of the frond. The cells in these niduses become partitioned each into four chambers, and the latter contain protoplasts, which surround themselves with membranes and become spores. The spores are set at liberty as a consequence of the solution of the walls of the chambers, and they occupy, in the form of a fine powder, little vesicular cavities in the tissue of the pinnules. The epidermis of these pinnules now serves as the wall of the cavities, *i.e.* of the sporangia.

Each plant in the group of the Ophioglosseæ exhibits two kinds of frond: the one kind develops no spores and has the appearance of a green foliage-leaf; the other produces sporangia, which are arranged either like bunches of grapes or in spikes consisting almost entirely of the sporangia (see fig. 189[8]). A similar arrangement may be observed also in many Ferns belonging to other divisions, as, for instance, in the genera *Allosorus*, *Struthiopteris*, and *Blechnum*, representatives of which occur in the European Flora as well as in others. In other cases, such as the Flowering Fern (*Osmunda regalis*), for example, sporangia are only formed on the upper portion of a frond, whilst the lower segments are foliaceous. A very peculiar form is that of *Rhipidopteris peltata*, a fern indigenous in the mountainous regions of Mexico (see fig. 189[4]). Besides the flat, fan-shaped fronds which produce no sporangia, other fronds shaped like funnels or shallow bowls are developed, and the spore-cases are produced from the epidermal cells in the hollows of these fronds.

In the last case it is worthy of note that the sporangia are formed on the upper

surface of the frond, for this is of very uncommon occurrence. They are usually situated on the under surface of the frond, the reason being that they are thus best sheltered from both rain and sun. Most instances exhibit in addition a further safeguard against excessive moisture or desiccation in the form of a special awning covering the sporangia. This awning is either an outgrowth from the cells forming the apex of the sporangiferous cushion or peg, and takes the form of a delicate membrane stretched over the whole sorus and known as an *indusium*, as in our male Shield Fern (*Aspidium Filix-mas*), or else small, scale-like leaflets spread themselves over the sporangia, as in the Gleichenias (fig. 189 [9]), to which reference has already been made, and in the no less remarkable Lygodiums and Davallias. Sometimes five or six squamous leaflets stand in a circle round the sporangia and envelope them so that the whole looks deceptively like a closed flower, as in the genera *Schizocæna*, *Hymenocystis*, and *Diacalpe*; or, these leaflets form a sort of box, which opens with a lid, as in *Cibotium*. In other cases, again, membranous bands or borders grow up from the surface of the frond, and the sporangia, which are arranged in a long line, are covered over by them, as occurs in *Lindsaya* and *Blechnum*; or, the margin of the frond is split and the sporangia are hidden in the narrow cleft thus made, as in *Vittaria* and *Schizoloma*. Often the margin of the frond is folded over, thus covering the sporangia, which are here developed on raised cushions; *Allosorus*, *Ceratopteris*, *Ceratodactylis*, *Parkeria*, and many other genera exhibit this formation. The extreme variety prevailing in this class of adaptation is connected with differences in the climatic conditions of the habitats where the plants in question live. Any attempt to deal with individual contrivances here would lead us too far.

The Rhizocarpeæ are a group nearly allied to Ferns, and they naturally follow the same lines as Ferns in the formation of their spores and sporangia. *Salvinia* reminds one to some extent of the Hymenophyllaceæ, at any rate as regards the outgrowth of an annular wall below the sporangia (the latter being in this case also borne on a fusiform axis), and also as regards the development of this wall, which becomes closed at the top into a complete box enshrouding the sporangia. *Marsilea*, on the other hand, exhibits stalked, bean-shaped capsules with cavities in which the sporangia are formed on raised cushions.

The Club-mosses (Lycopodiaceæ) also bear a striking resemblance in their mode of spore-formation to Ferns, especially to the various species of *Lygodium* and *Lygodictyon*, genera of which mention has already been made. The first rudiments of the sporangia are swellings at the base of the little squamiform leaves, or on the axis just at their insertion. The internal tissue of this protuberance is marked off in the form of a roundish ball. The cells constituting the ball separate and then become segmented each into four chambers, the walls of which are subsequently dissolved. The protoplasts within the chambers inclose themselves in membranes and become free spores. The epidermis originally clothing the swelling persists, and now forms the wall of a bean-shaped sporangium containing loose spores. The sporangium subsequently opens by means of a lid like a box.

Horse-tails exhibit a process of spore-formation quite peculiar to themselves. Two species of this group—namely, *Equisetum arvense* and *E. sylvaticum* are shown in figs. 190[2] and 190[7]. At the top of the hollow stem there is a spike of peltate scales borne on short stalks and arranged in whorls, each of which must, in consideration of its origin, be looked upon as a metamorphosed leaf (*cf.* fig. 190[3]).

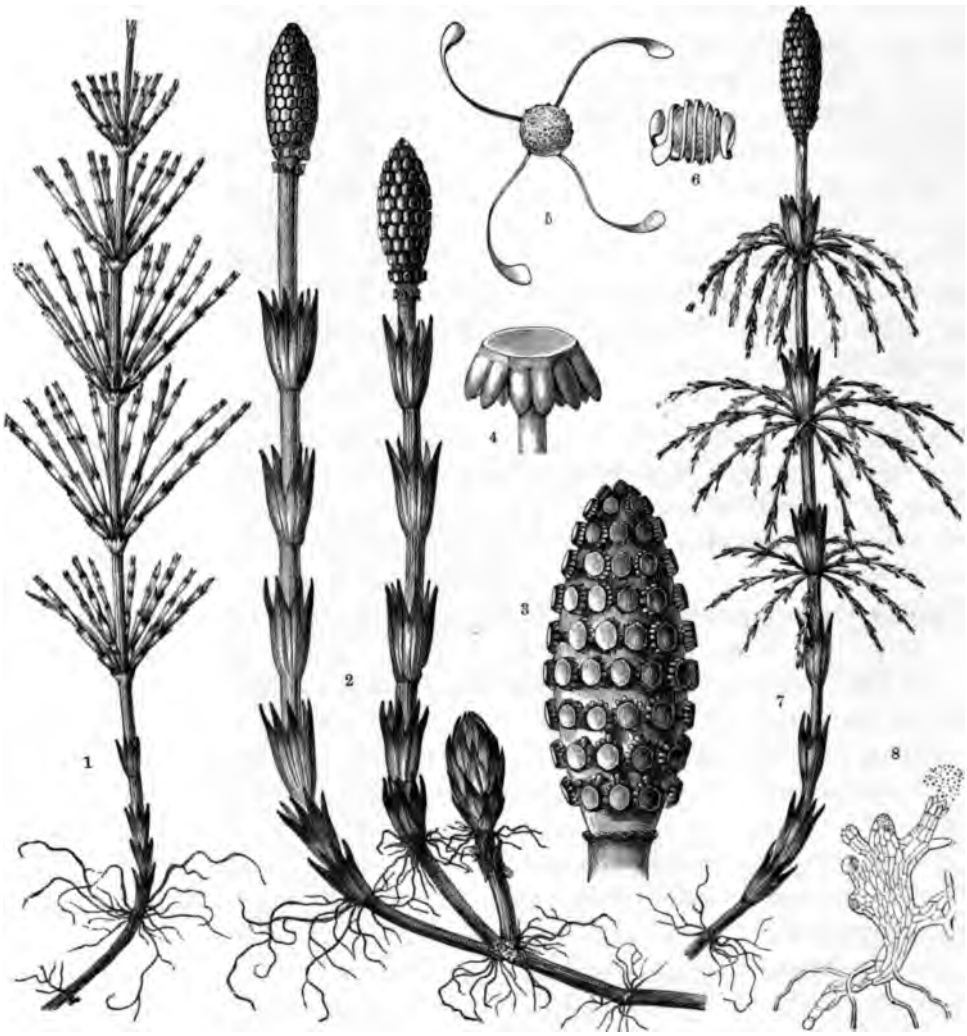

Fig. 190.—Horse-tails.

[1] Summer Shoot of *Equisetum arvense*. [2] Vernal fertile Shoot of *Equisetum arvense*. [3] Spike of whorled sporangiophores from the same *Equisetum*. [4] A single sporangiophore. [5], [6] Spores. [7] *Equisetum sylvaticum*. [8] Prothallium of a Horse-tail. [1], [2], [7] natural size; [3] × 3; [4] × 6; [5], [6] × 25; [8] × 30.

On the inner surfaces of the scales—*i.e.* those turned towards the axis of the spike—little warts arise, which develop into sporangia (*cf.* fig. 190[4]). The outer cell-layers of these multicellular warts become the walls of the sporangia, whilst the inner tissue breaks up into cells. These cells then divide into four cells, each of which becomes a spore.

The last division of plants wherein the spores are formed deep down in a tissue is that of the Muscineæ, which include Mosses and Liverworts. In these plants the spore-producing generation consists of a cellular body, which has arisen from the fruit, is usually seated on a stalk, and in shape is cylindrical, pyriform, or more or less spherical (*cf.* figs. 191 [3, 4, 7, 8, 15]). We must here remark, by the way, that botanists used formerly to look upon this sporogenous generation of the Moss erroneously

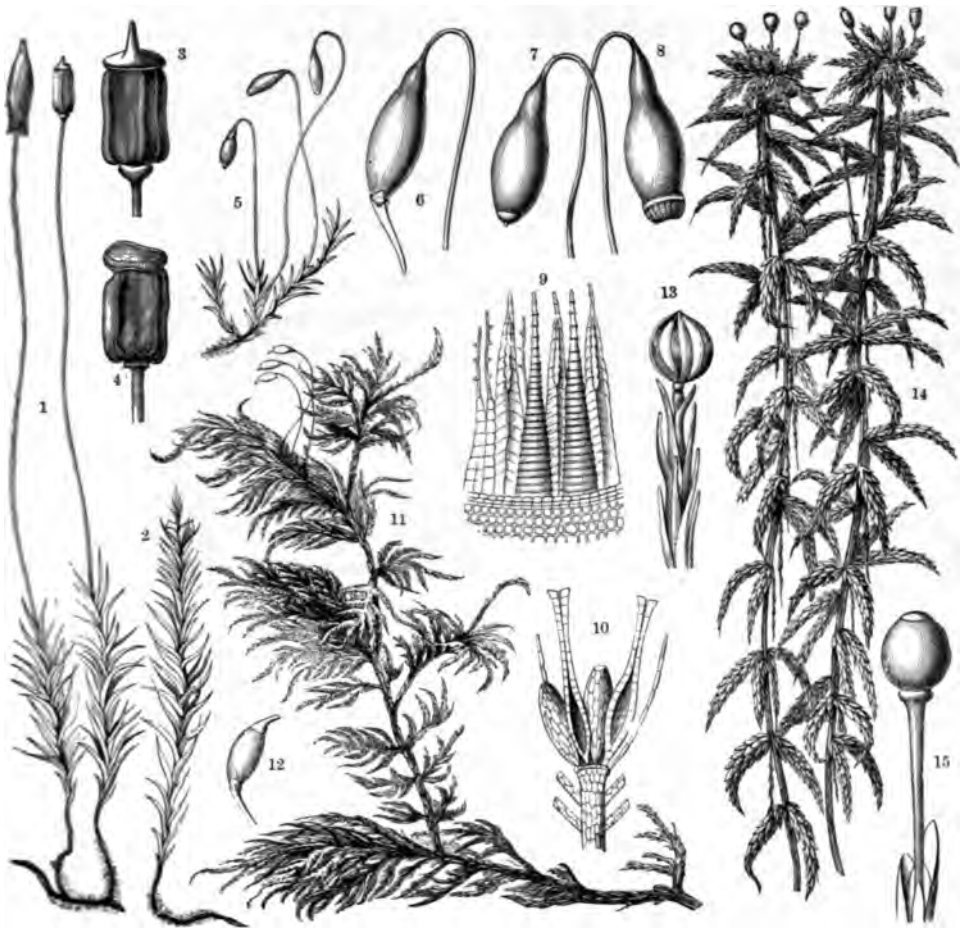

Fig. 191.—Mosses.

[1] ***Polytrichum communs***, the sporogonium to the left concealed by the cap, the sporogonium to the right exposed. [2] The same Moss in an earlier stage of development. [3] Sporogonium of *Polytrichum communs* with its lid. [4] The same after the lid has fallen off. [5] *Bryum cæspiticium*. [6] Sporogonium of the same Moss with its cap. [7] The same without the cap, but with the lid still on. [8] The same after removal of the lid, showing the teeth (peristome). [9] A piece of the peristome. [10] Antheridia, Archegonia, and Paraphyses of *Bryum cæspiticium*. [11] *Hylocomium splendens*. [12] Sporogonium of *Hylocomium splendens*. [13] *Andræa rupestris* with burst sporogonium. [14] *Sphagnum cymbifolium*, its spherical sporogonia still covered by their lids in the left-hand specimen. [15] A single sporogonium of the same Moss. [1, 2, 5, 11, 14] natural size; [3, 4, 6, 7, 8, 12, 13, 15] × 5; [9, 10] × 150.

as the fruit itself. The only structure rightly to be considered as the Moss-fruit is that in which the embryo is produced as a result of fertilization. If afterwards a new generation springs up from the embryo which has been formed in the interior of the fruit, this generation cannot any longer be described as a fruit even in cases

where it remains permanently connected with the mother-plant, as happens in Mosses.

The cells composing the tissues of the cylindrical, pyriform, or spherical body above referred to develop in a variety of ways. Those situated near the outer surface form the wall of a receptacle, and those in the interior, which serve as a filling to the receptacle, form the spores. The process of spore-formation is here much the same as in Ferns. The cells of the central mass, at first united into a tissue, in time become isolated; each divides into four, and the spores are ultimately developed from these protoplasts. The spores are then left free in the form of a fine powder within the receptacle, which is called a sporogonium. In most Liverworts, a group nearly allied to the Mosses, certain other cells having a curious structure are formed from the internal tissue besides the spores. These are the so-called "elaters", and they serve to scatter the spores. In a few Mosses a sort of central column remains in the middle of the sporogonium in addition to the spores when the whole is mature. Externally the sporogonia of Mosses differ very little from the cellular bodies out of which they were developed; like them, they are spherical, pear-shaped, or cylindrical as the case may be. But the part which subsequently opens and liberates the spores at the proper time exhibits in its more minute anatomy considerable differentiation. This subject and that of the elaters mentioned above will be again referred to in the section devoted to the distribution of spores.

As with the sporangia in Ferns, so also in Mosses the sporogonia are protected during development from injurious external influences, especially desiccation, and are wrapped in coverings which vary considerably according to their origin. In Mosses a kind of cap is usually to be seen covering the young and tender sporogonium (see fig. 191 [1]), and this structure has its origin in the fruit from which the sporogenous generation (or *sporophyte*) has sprung, the coat of the fruit being torn away and its upper part carried up in the form of a cap by the sporophyte during its growth from the embryo. Later on, when the sporogonium is no longer in need of protection, and the presence of a cover would be detrimental in that it might prevent the spores from being scattered, the cap is cast off.

All the spores hitherto discussed originate within a tissue, and their history involves the conversion of the protoplasmic contents of each compartment of the reproductive part of the tissue into a spore. A second group of spores is composed of those which arise from the breaking up of the protoplasmic contents of tubular, club-shaped, or spherical cells not united in tissues, and are set free from their birthplaces as soon as they are formed. The cells thus constituting the mother-cells of spores may, by analogy, be conveniently termed sporangia. The process of formation of spores within them appears to be much simpler than in Ferns, Club-mosses, Horse-tails, Mosses, and Liverworts. Speaking generally, the only striking differences occurring in these cases are such as affect the number and shape of the spores which escape from a sporangium.

As described in the first volume of this work (*cf.* vol. i. p. 23, and fig. 25A, *a–d*),

the filamentous organism *Vaucheria* produces a single comparatively large green spore in each of the club-shaped outgrowths developed by the tubular branches of the plant, and each spore thus formed is able, when free, to swim about by means of its numerous short cilia. On the other hand, the mould-like Saprolegniaceæ, which live under water upon decaying animals, develop a large number of colourless spores in their clavate filaments, and these after escaping from the tubes whirl about in the water by means of two long revolving cilia (*cf.* fig. 192). In both

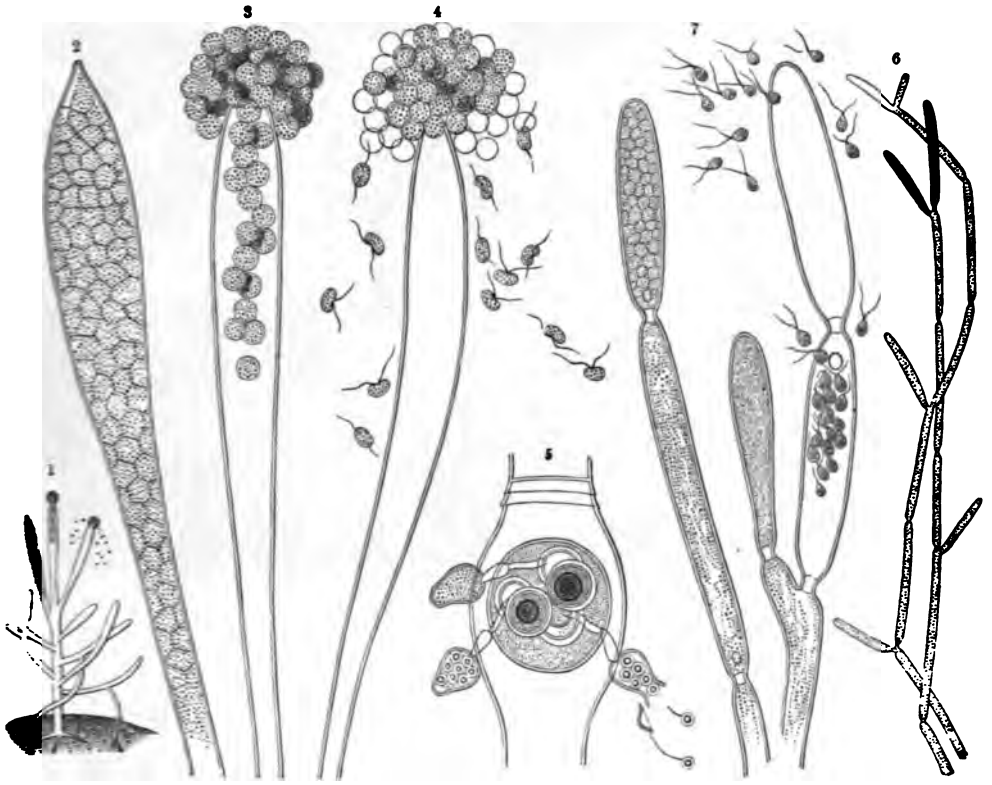

Fig. 192.—Swarm-spores of Saprolegniaceæ and Chytridiaceæ.

[1] *Achlya prolifera*. [2, 3, 4] Development and escape of swarm-spores of *Achlya prolifera*. [5] *Chytridium Ola* parasitic upon the oogonium of *Œdogonium*; development and escape of swarm-spores. [6] *Saprolegnia lactea*. [7] Development and escape of the swarm-spores of *Saprolegnia lactea* (partly after De Bary and Pringsheim). [1] ×20; [2, 3, 4] ×400; [5] ×300; [6] ×100; [7] ×300.

these instances the spores themselves possess the power of movement and of swarming about in water, whence they are called "swarm-spores". The name "zoo-spores" (ζῷον=animal) has also been applied to them on account of their decided resemblance in form and behaviour to certain Infusoria.

The delicate, profusely-branched mycelia of the Moulds, included under the name Mucorini, give rise to special filaments which grow straight upwards. These erect hyphæ divide into two cells. The upper cell becomes a spherical bladder, and the under a long slender stalk, the upper end of which protrudes in the form of a hollow stopper into the bladder supported by it (*cf.* fig. 193 [2]). The protoplasm in the upper vesicular cell breaks up into a large number of spores and thus

becomes a sporangium. The increase in weight of the sporangium causes the filiform stalk to bend; the sporangium bursts, and the spores, together with the clear fluid in which they are suspended, issue through the rent in the sporangium (*cf.* fig. 193[1]).

In the Moulds of the family of the Mucorini the sporangia are for the most part

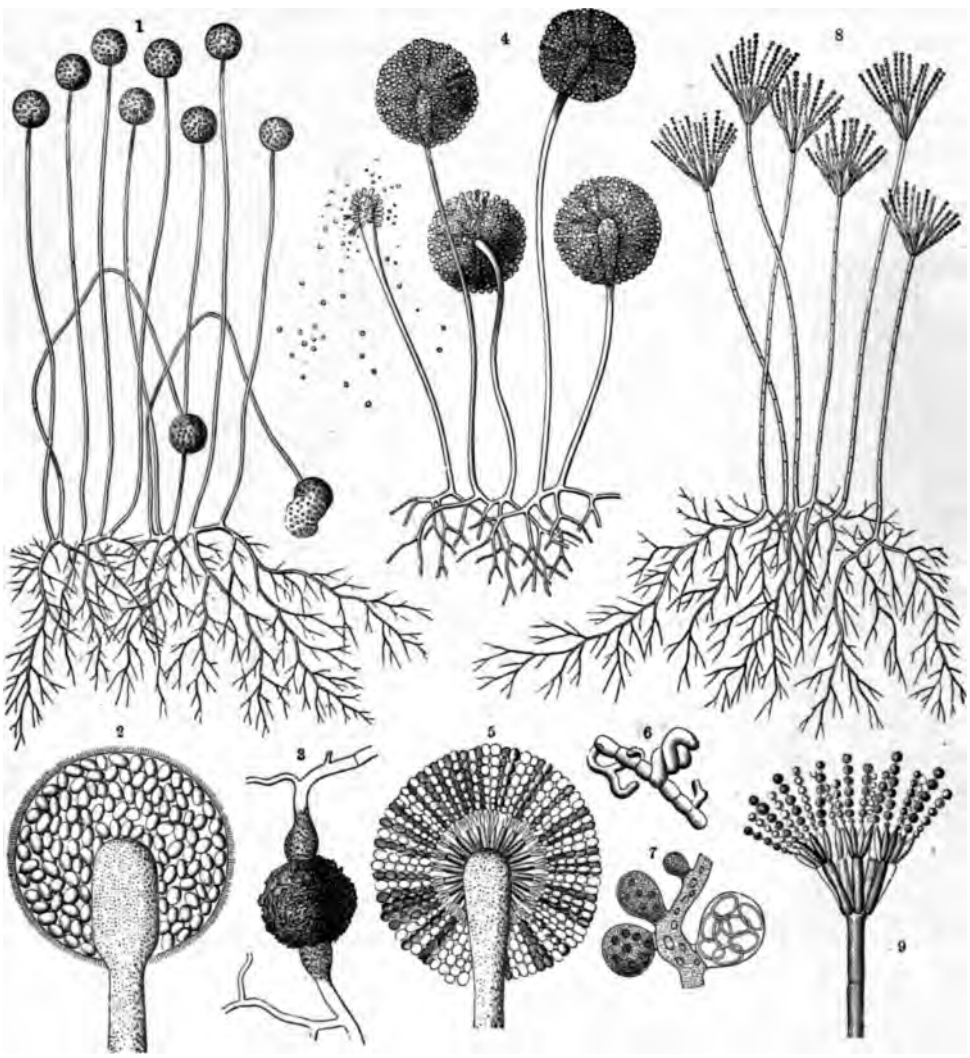

Fig. 198.—Moulds.

[1] *Mucor Mucedo*; ×40. [2] Longitudinal section of a sporangium of *Mucor Mucedo*; ×260. [3] Fruit-formation in *Mucor Mucedo*; ×180. [4] *Aspergillus niger*; ×30. [5] Longitudinal section of a sporophore of *Aspergillus niger*. [6] Fructification of *Penicillium crustaceum* (after Brefeld). [7] Fruit-formation in *Aspergillus* (after Eidam). [8] *Penicillium crustaceum*; ×40. [9] Sporophore of *Penicillium crustaceum*; ×200.

closely crowded together, but they are never walled in by a tissue or surrounded by any particular envelope. They are, moreover, always separate, and have the appearance of a miniature plantation. A different state of affairs is found in that group of Fungi known as the Ascomycetes, a group which includes, amongst well-

known plants, the genera *Morchella* and *Helvella* (*cf.* fig. 194), Lichens, and also several mould-like forms, notably the Erysipheæ, which produce Mildew, and *Claviceps*, which is the cause of Ergot of Rye. In these plants the ends of the hyphæ stand up from restricted areas of the mycelium, some in the form of long clavate tubes, some as delicate filiform paraphyses, the group of tubes and paraphyses being surrounded by other cellular structures in such a manner that the whole has the appearance of a dish or cup or capsule. The protoplasm in the tubes breaks up and forms either ellipsoidal bodies arranged usually in linear series (*cf.* fig. 194[2]) or long fascicled threads, which, whilst still inclosed in the

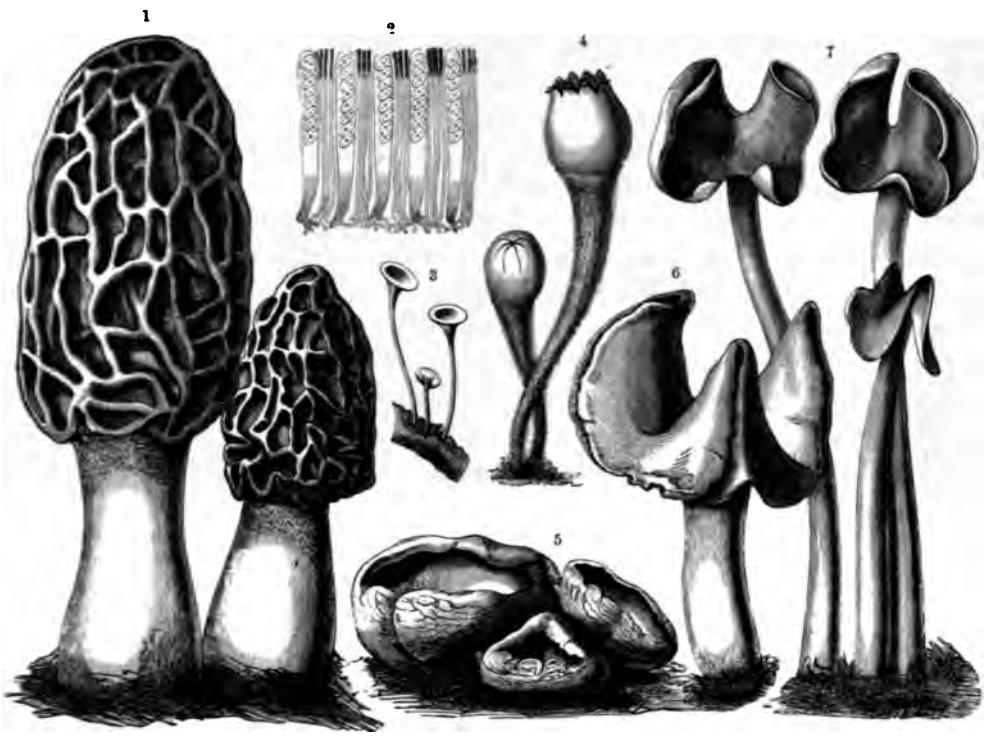

Fig. 194.—Discomycetes.

[1] The Morel (*Morchella esculenta*). [2] Longitudinal section from the hymenium of *Morchella esculenta* showing five filaments each containing eight spores and filiform paraphyses in between them. [3] *Helotium Tuba*. [4] *Anthopeziza Winteri*. [5] *Peziza vesiculosa*. [6] *Helvella Infula*. [7] *Helvella fistulosa*. 1, 4, 5, 6, 7 natural size; [2] ×4; [3] ×120.

tubes, put on a stout cell-wall. The name of *asci* (ἀσκός = a leather bag) has been given to these sporangia, and *ascospores* to the spores which they contain. They are destitute of cilia, the distinguishing mark of zoospores, and have no power of independent motion after their extrusion from the tubes, which takes place through a rent at the top.

There is great variety in the mode of grouping, as also in the envelopment of the sporogenous tubes in different genera and species. When the tubes grow from the bottom of flask-shaped excavations or pits, the whole structure is spoken of as a *perithecium*; if they stand in a shallow patelliform cavity or on the surface the

term used is *apothecium*. Perithecia and apothecia have been erroneously called fruits also. The same principles must here be applied as governed our consideration of Ferns and Mosses. Even if the genesis of perithecia and apothecia is really preceded by a process of fertilization, still the only part properly to be called a fruit is the tissue in which one or more protoplasts have become embryos in consequence of the act of fertilization. The outgrowth from this fruit is precisely the new generation; and it does not matter at all whether this new sporogenous generation preserves its connection with the previous fruit-forming generation or not. Perithecia and apothecia, and, in general, all so-called fruits in the Ascomycetes are therefore equivalent to the sporogonia in Muscineæ and to the sporangiferous plants in Horse-tails, Club-mosses, and Ferns.

We shall place together in a third group all spores which arise neither singly in the cell-compartments of a tissue nor through the breaking up of the protoplasm within a tube, but by abstriction and abjunction. The process of spore-formation in these cases is as follows:—The protoplasm, which is inclosed in a cell-wall, produces an internal partition whereby it is itself divided into two halves, and the cell-cavity into two chambers. As soon as this has taken place the partition-wall splits and the two cells fall asunder. If the cell which undergoes the process of bipartition is in the form of a blind tube or sac, and if the partition is intercalated near the tip of the sac, the effect produced is as though the end of the sac had been tied off or abstricted and had then dropped. The part remaining behind now constitutes another blind sac, and in some genera the process of abjunction from the extremity may be repeated over and over again. *Basidium* is the name given to a closed sac of this kind from which spores are abstricted, it forming in a manner a base for the spores. This term has hitherto only been employed by botanists in relation to the so-called Basidiomycetes (which includes the Fungi known as Mushrooms and Toadstools), but it is justifiable to extend its application to all other structures which play the same part.

Abstriction of spores is exhibited at its simplest in the plant known as the Rust of Wheat, which at a certain stage of its development lives as a parasite in the green tissue of the leaves of our species of Wheat. For the purpose of spore-formation tufts of hyphæ project beyond the surface of the infested leaves. At the extremity of each hypha, which is in the form of a closed sac, a single spore of comparatively large size is developed; and after the fall of this one spore the hypha or basidium has lost the power of abstricting others.

A similar phenomenon is observed in the Fungi belonging to the genera *Hydnum*, *Polyporus*, *Agaricus*, and *Clavaria*, of which several examples are represented in fig. 195. Their basidia are club-shaped, and terminate in four slender filaments, the so-called *sterigmata*, and from the end of each sterigma one spore is abjointed (fig. 195[7]). These basidia, together with a number of slender sac-like tubes, to which reference will again be made when the Basidiomycetes are described in detail, beset certain structures projecting from the under surface of the cap-shaped sporophore — these structures being lamellæ or spikes or tubes

as the case may be. *Aspergillus niger* (see fig. 193[4] and 193[5]), a Mould living chiefly on the juices of fresh or preserved fruits, develops slender upright hyphæ with swollen ends, which bear numbers of short peg-like processes—the sterigmata—from which moniliform series of from five to eight spores are abjointed in

Fig. 195.—Basidiomycetes.

[1] *Clavaria aurea.* [2] *Dædalea quercina.* [3] *Marasmius tenerrimus.* [4] *Marasmius perforans.* [5] *Craterellus clavatus.* [6] *Amanita phalloides.* [7] Clavate basidia with filamentous sterigmata, from the ends of which spherical spores are abjointed (from the hymenium of *Amanita phalloides*). [8] *Hydnum imbricatum.* [9] *Polyporus perennis.* 1, 2, 3, 4, 5, 6, 8, 9 natural size; [7] ×250.

rapid succession. These spores at first hang loosely together, and are arranged like strings of pearls, but collectively these rows of spores form a spherical head. A shock of any kind, especially the disturbance occasioned by currents of air, will cause a severance of the spores, and the entire sphere consequently falls to pieces.

Nothing then remains but the hyphal filament with its swollen end beset with pegs and looking like a club armed with spikes (*cf.* fig. 193[4]).

Also in *Penicillium*, the commonest of all Moulds, the spores are abjointed from the sterigmata in moniliform rows; but in this case the erect hypha which bears the spores is septate and not clavate at the extremity, and terminates in forked branches, so that the chains of spores are grouped like the hairs in a camel's-hair pencil. A species of *Penicillium*—viz. *P. crustaceum*—is represented in fig. 193[8] and 193[9]). In the Peronosporeæ, to which class belongs the parasite *Cystopus candidus*, celebrated for its fatal effects on cruciferous plants, moniliform rows of spores are abjointed from the basidia without the intervention of sterigmata. The mode of arrangement of the chains of spores in this parasite is, however, not quite like that in either *Penicillium* or *Aspergillus*.

A further diversity in this kind of spore-formation by process of abjunction is introduced by the presence in several families of plants of special envelopes surrounding the abjointed spores. Particular cases of this are afforded by Gasteromycetes (Puff-ball family) and Florideæ (Red Seaweeds) and by that stage in the development of the Rust-Fungus which is known by the name of *Æcidium*. The æcidia make their appearance in the form of structures growing out from a mycelium infesting the green tissues of leaves. The basidia are formed by the ends of hyphæ which stand up in dense crowds. Moniliform chains of spores are abjointed from the basidia and are enveloped by a sporangium-like wall developed from the cells surrounding the basidia. It is not till this enveloping capsule bursts that the spores are set free and can be distributed.

In the large Puff-Ball family (Gasteromycetes) the same process takes place, but the basidia and spores are not arranged so regularly, and amongst the spores are to be found other hair-like, cellular structures which constitute what is termed a *capillitium* and are of especial importance in relation to the distribution of the spores. Florideæ develop their spores within receptacles peculiar to themselves, which frequently resemble urns or capsules, and might be designated sporangia for the sake of terminological uniformity. The spore-filled "sporangia" of Florideæ, like those of Muscineæ—and in particular of Liverworts—are to be conceived as a separate generation, and, moreover, as a generation springing from cells which have undergone fertilization and have thereby been converted into fruit. The description of the process of fertilization must be postponed to a later section of this book; we have only to notice here that short cells are put forth as branches from the fertilized cells, and that some of these branches abjoint clusters of spores whilst the others develop into a sheath enveloping the assemblage of spores thus produced.

Under the name of Thallophytes are included all such plants as are destitute of vascular bundles and therefore are never developed into real *plant-bodies* (*cf.* vol. i. pp. 590–592). It often happens that Thallophytes form, in addition to the unicellular brood-bodies to which the name of spore must be limited, cell-aggregates which sever themselves from the thallus and become independent, the genesis of

which has not been in any way a result of fertilization. These aggregates of cells are, in a manner, structures intermediate between the unicellular spores and the buds, differentiated into axis and leaves, which occur in vascular plants. They are portions of the thallus which produced them, and are either very like it or assume the same form as soon as their further development is complete. Hence the most appropriate name for these bodies is that of *thallidia* (θαλλός = young shoot; εἶδος = a likeness). They are also known as *gemmæ*. Thallidia are some-

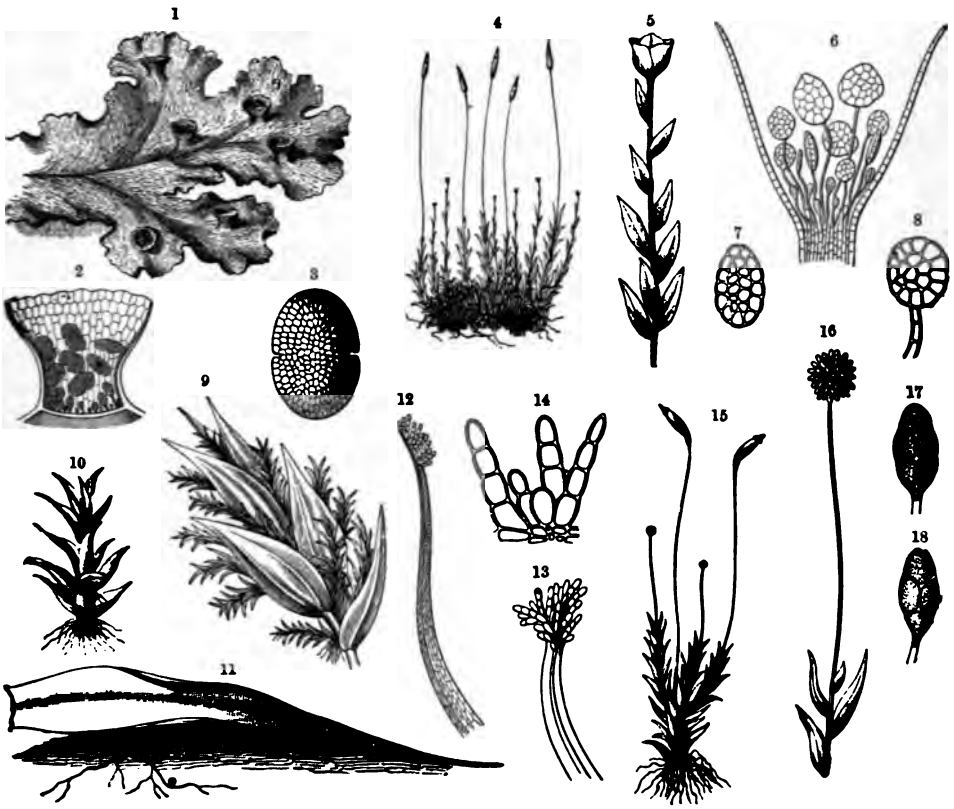

Fig. 196.—Thallidia of Muscineæ.

[1] *Marchantia polymorpha* with cups containing thallidia or gemmæ. [2] Longitudinal section of thallidial or gemmiferous cup. [3] A single thallidium. [4] *Tetraphis pellucida*. [5] A stem of *Tetraphis* bearing a cup containing thallidia. [6] Longitudinal section of a thallidial cup. [7, 8] Isolated thallidia of *Tetraphis*. [9] A stem of *Leucodon sciuroides* with brood-bodies. [10] A brood-body set free from the stem. [11] Development of a brood-body from the rhizoids of a leaflet torn from *Campylopus fragilis*. [12, 13, 14] Development of thallidia at the apex of a leaf of *Syrrhopodon scaber*. [15] *Aulacomnion androgynum*. [16] A stem of the same bearing thallidia. [17, 18] Single isolated thallidia. [1] natural size; [4, 16] × 2; [2, 12, 13] × from 8 to 15; [3, 6, 9, 10, 14] × from 20 to 40; [3, 7, 8, 17, 18] × 120.

times in the form of rows of cells, as, for example, those developed on the leaflets of the Moss *Syrrhopodon scaber* (see figs. 196 [12, 13, 14]); sometimes they are nets, as in the Water-Net (*Hydrodictyon*, see figs. 197 [1, 4, 5]). In the Moss *Tetraphis pellucida* (see figs. 196 [4, 5, 6, 7, 8]) they occur as plates of cells, and in other cases they assume the form of globular or ellipsoidal lumps of tissue, as, for instance, in the Moss *Aulacomnion androgynum* (see fig. 196 [15, 16, 17, 18]). Sometimes the number of cells associated

in a brood-body of the kind is limited to two, as is the case in the so-called "teleutospores" of the Rust-Fungus; whilst those of Florideæ sometimes have four cells and are known as "tetraspores". Again, in other cases hundreds of cells are associated together to form a thallidium, an instance of which is afforded by the brood-body or gemma of *Marchantia* (see fig. 196 [1, 2, 3]). The "soredia" of Lichens must also be brought under this head—by the term soredia being understood certain bodies which arise upon the thalli of Lichens and consist of one or more green cells wrapped in a net-work of colourless hyphæ (see vol. i. p. 248).

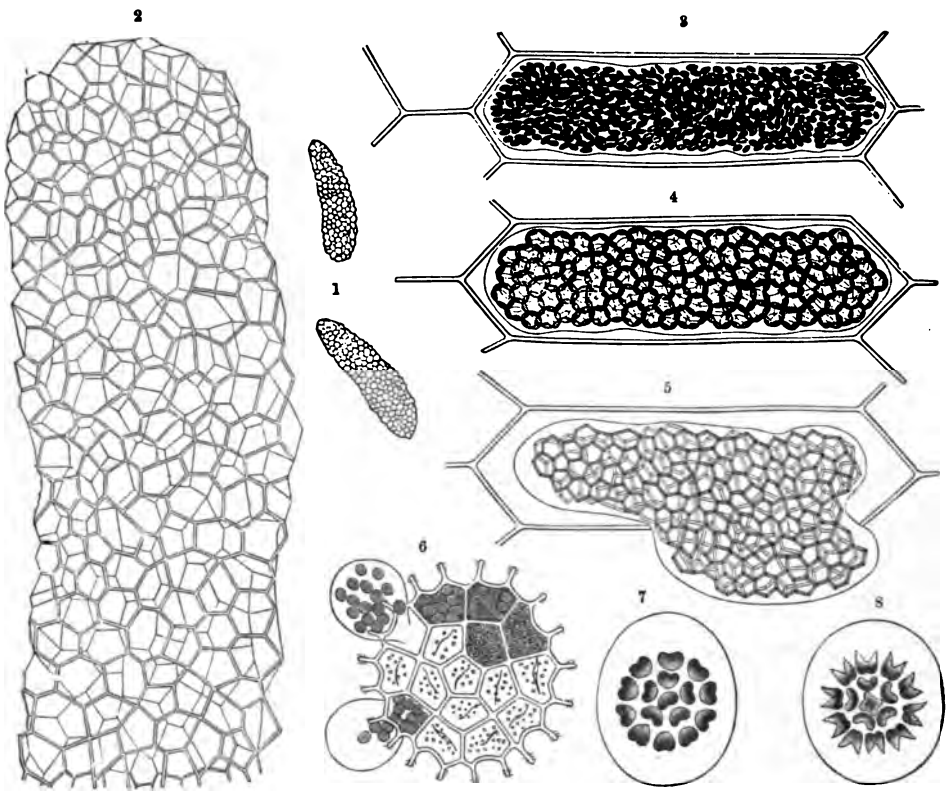

Fig. 197.—Formation of Thallidia in the cells of *Hydrodictyon* and in those of *Pediastrum*.

[1] Water-Net (*Hydrodictyon utriculatum*), natural size. [2] A piece of the Water-Net; × 50. [3, 4, 5] Development and escape of a reticulate thallidium; × 300. [6] *Pediastrum granulatum*; development and escape of thallidia; the lightly-dotted cell chambers already vacated. [7, 8] Thallidia of *Pediastrum* after their escape; × 240.

Thallidia may originate in the interior of a cell-cavity of the parent-plant and escape in the form of complete, though extremely minute, cell-aggregates. Instances of this are afforded by the Water-Net (*Hydrodictyon utriculatum*), which is shown in fig. 197 [5], and by *Pediastrum granulatum* (fig. 197 [6]), an organism of frequent occurrence in pools. The alternative method of formation of thallidia is by the severance of groups of superficial cells, which, after an interval of peregrination of variable duration, fasten on to some spot or other and found a new colony. In many Liverworts and Mosses special pockets and

cups are produced, within which thallidia are continuously developed in the manner shown in figs. 196 [1, 2, 3, 4, 5, 6, 7, 8].

The formation of these brood-bodies by Lichens and Mosses may be induced by wounds or mutilations affecting the plants in question; but the stimulus is not here susceptible of being so clearly and surely inferred from its effects—and perhaps has hardly yet been so carefully investigated—as in the case of trees, shrubs, and herbs, which, being planted on a large scale, have afforded experience for centuries with the result that the practice of inducing the formation of buds by mutilation and of using them for the purpose of artificial propagation is extremely common in cultivation. Parasitic thallophytes receive an evident stimulus to the formation of brood-bodies upon the death of their hosts. As long as the host-plant is healthy and vigorous the parasites keep their hyphæ and suckers buried within the nutrient tissue. They there consume all there is to consume, increase in size, and thread their way through wood and green tissue in ever-widening circles—but without ever forming brood-bodies. Not until the host is quite exhausted and languishing at death's-door does the parasite, to avoid the danger of perishing with its foster-parent, provide for its departure from the ruin, and it is then in the form of brood-bodies that it escapes from the tissue it has ravaged. Here and there some of the tubular cells grow quickly from the interior of the dying tissue of the host-plant and emerge to the surface through stomata or rotten cell-walls. All the substance contained in the cells of the parasite becomes concentrated at these new foci of formative activity, and here masses of spores and thallidia are developed and abstricted at the very points where most extensive distribution is rendered possible by currents of air and water. Thus, the parasite is resolved into a number of brood-bodies and abandons the mansion which it has brought to destruction.

BUDS ON ROOTS.

Just in front of the house in which I am writing there used to stand years ago a great Aspen. The tree was felled, the axe being laid so close to the earth that only a stump projecting a few centimetres above ground was left. In the following spring the stump became the centre of quite a grove of Aspens, slender shoots having pushed through the grass over a large circular area round the stump. At first the shoots appeared one by one, then by dozens, and at last by hundreds at a time. They grew up into trees, and now, instead of the single Aspen, there is a little wood composed of trees which have not sprung from seed, but from the subterranean roots of the felled Aspen. Before the old tree had been deprived of its trunk and foliage its underground roots produced lateral roots only, which grew in a plane beneath and parallel to the surface, and continued to spread so long as they did not encounter any insuperable obstacle. Suddenly there was a change in the processes going on in this root; its formative energy was no longer devoted to the development of lateral roots, but was directed

to the construction of buds from which green leafy shoots sprang up above the surface of the ground.

A forester of the old school, whose attention I drew to the above phenomenon with a view to ascertaining how he would explain it, told me that when the tree was cut down the flow of sap destined for the nourishment of the trunk and its crown of foliage was arrested in the roots underground, and thereupon sought an outlet elsewhere. Lateral roots having become useless, the diverted juices did not form them, but instead sent a great number of delicate shoots above the ground, because this was the only manner of preserving the life of the Aspen. At first sight this may seem to some people a foolish answer, and I have even heard it called absurd. Nevertheless we are obliged, after impartial consideration, to admit that we are not in a position to give any explanation which is not essentially the same. If we conceive the living protoplasts in the formative tissue of the roots as being the "juices" referred to by the forester, there is no longer any difference between his explanation and that given by Science. At the very spots where formerly lateral roots would have been developed, leafy stems are produced. The same protoplasts which now work at the construction of a bud would, if the tree had not been cut down, have fashioned a lateral root. That this alteration in active function was caused by the felling of the tree is certain, although no mechanical explanation of this stimulus can be given. The only possible source of excitation seems to be the checking of the egress of formative material stored in the roots in the direction in which it was formerly accustomed to flow.

Another special point of interest connected with the history of this Aspen is that for the most part the roots, after giving rise to a series of shoots, died and decayed, whilst the shoots developed into separate and independent trees, each furnished with roots of its own, so that they look as if they had been deliberately planted in the earth in rows. As a matter of fact, however, the Aspen itself produced these saplings from its subterranean portions, and planted them out, thus not only renewing its own youth but multiplying. For such multiplication it is evidently necessary that some cell in that part of the root which possesses the power of growth should form the starting-point or rudiment of a new shoot. The cell chosen for the purpose divides into daughter-cells, and these again become subdivided; but several adjacent cells also participate in the new fabrication, and we can picture to ourselves the process as the action of a group of protoplasts located within the limits of the living and formative tissue of the root, which separate themselves off from the rest and form a confederation of mutually helpful associates with the common function of constructing the new shoot. Neither the protoplast in the mother-cell of the young shoot nor the adjacent protoplasts undergo any stimulation by neighbouring cells before beginning their work. No process of pairing takes place. The phenomenon of renewal and multiplication of the Aspen which goes on before our eyes must therefore be classed as a case of asexual reproduction. The fact that a single root of the Aspen, instead of producing one sapling

only, gave rise to ten, obliges us to suppose that these protoplasts of the growing tissue of the root, which separated themselves off under the influence of the new conditions created by the felling of the tree, arranged themselves in ten groups and each group from that time forth devoted itself to the new task of furthering the growth of the shoot developing at its centre. On investigation we find that these aggregations of cells are invariably situated in the deeper layers of the rind. In the first place a delicate tissue is developed from a particular cell which dominates the entire group and governs the process of construction. This tissue pushes outwards, on the one hand, towards the superficial layers of the rind, whilst, on the other hand, it sends a shaft inwards into the cambium layer of the root. Immediately afterwards vascular bundles are developed, and the shaft-like rudiment of the young bud is through them placed in connection with the woody tissue of the root, and when all this is finished the rind is finally broken through, and a bud clothed with leaves behind its growing point bursts out through the opening.

These buds, and the shoots arising from them, are termed radical buds and shoots. They are anything but rare, and it would be an error to suppose that they only occur on the Aspen because that tree has been chosen to illustrate the subject. Not only a great number of trees, but also many shrubs, and a host of herbaceous plants, great and small, exhibit this kind of revival and multiplication, and for many species it is the safest and most fruitful mode of reproduction. It would also be wrong to suppose that radical buds only arise when the aërial parts of the plant concerned have been injured or destroyed in consequence of some unusual occurrence. A shock of the kind is certainly the most frequent cause; but it is equally certain that of trees and shrubs not a few develop rudimentary buds on their roots when their time comes—*i.e.* when they have become decrepit, and one branch after another is dying—without their having suffered any injury from worm or weather, or from the woodman's axe. A profuse after-growth of young plants always springs from the roots and surrounds old and dry trees of the following kinds:—the Aspen (*Populus tremula*), the Tree of Heaven (*Ailanthus glandulosa*), the Tulip-tree (*Liriodendron tulipifera*), and the Osage Orange (*Maclura aurantiaca*), and the same statement applies to the following shrubs when they begin to wither—the Raspberry (*Rubus Idæus*), the Sea-Buckthorn (*Hippophae*), the Hawthorn (*Crataegus*), the Barberry (*Berberis*), the Lilac (*Syringa*), and the Rose (*Rosa*), and to many other woody plants; whereas, no such "breaking" from the root is seen on young specimens of the above unless there has been some previous injury to the parts above ground.

The budding power of roots is made use of by gardeners for the purpose of artificial propagation. They cut pieces from the roots of the plants they wish to multiply and insert them in soil which is kept moist, and they may then count almost with certainty upon the development of several buds on each separate piece of root. This mode of propagation by root-cuttings or slips, as they are called, is attended by particularly successful results when applied to the flowering trees or shrubs of *Cydonia Japonica, Paulownia imperialis, Tecoma radicans, Dais cotoni-*

folia, and to various species of *Acacia*, *Halesia*, *Hermannia*, and *Plumbago*. Moreover, the development of buds on roots is observed to take place not only in trees and shrubs, but also in herbaceous plants; and, indeed, in some it is of regular, annual recurrence. As instances of this may be mentioned the Dwarf Elder (*Sambucus Ebulus*), *Asclepias Cornuti*, *Sophora alopecuroides*, *Lepidium latifolium*, the Dock (*Rumex Acetosella*), various species of the Toad-flax and Spurge (*e.g. Linaria pallida*, *L. genistæfolia*, *L. vulgaris*, *Euphorbia Cyparissias*), and several Composites and Pelargoniums. In another series of herbaceous plants the phenomenon occurs exceptionally as a result of special external conditions, and chiefly in consequence of injuries, as, for example, in case of damage to the roots of certain Orchids (*Epipactis microphylla*, *Neottia Nidus-avis*), or of the Adder's Tongue amongst Ferns (*Ophioglossum vulgatum*). Nor must we omit to mention the buds which are formed on aërial roots. There is so regular a production of buds from the columnar aërial roots of tropical Fig-trees, and of leafy shoots from the buds thus developed, that at first sight one is inclined to take the root-columns for trunks.

BUDS ON STEMS.

Buds and shoots growing directly from a part of the stem are termed cauline buds and shoots. Any part of a stem may become the point of inception of a bud. The commonest positions occupied by buds are the regions of the stem which bear respectively scale-leaves and foliage-leaves, and this is especially the case with those buds which subsequently become brood-bodies. But also lower down and higher up buds are observed to develop, and do so, indeed, without the occurrence of any apparent injury or other assignable external cause. Thus, for instance, it frequently happens that buds are developed on the hypocotyl of the Scarlet Pimpernel (*Anagallis arvensis*), which abounds in our fields and kitchen-gardens, and the same is true of the species of Spurge (*Euphorbia Peplus* and *E. vulgaris*) which grow as weeds in company with the Pimpernel, and likewise of young Toad-flax plants (*Linaria vulgaris*), and of a few Umbellifers. These buds grow out immediately into green leafy shoots. In all probability the phenomenon occurs in many other plants besides, but hitherto the subject has received only cursory attention.

These buds on the hypocotyl are all the more worthy of notice because they emerge below the cotyledons and in no case from a leaf-axil, *i.e.* the angle formed by a leaf with the stem. In the region of the foliage-leaves it is comparatively rare for a bud to originate at any other spot than in the axil of a leaf. As instances may be mentioned the extra-axillary buds of the Nightshades (Solanaceæ), the buds in *Serjania*, *Medeola asparagoides*, &c., which spring laterally from the stem close to the foliage-leaves, and those in the Vine and Virginian Creeper (Ampelideæ), which are set opposite to the foliage-leaves. But even in these cases the positions of the buds, relative to the foliage-leaves of the stem, are always such as to be most naturally explained by the need of the former to obtain the formative materials produced in the green tissue of the leaves, in order to complete their own develop-

ment; and these materials are most directly conveyed to them if they are situated as near as possible to the spot where the vascular bundles of a green leaf lead into the stem.

When a large number of foliage-leaves are packed closely together upon a stem, it is scarcely possible for a bud to be developed in every axil. On such occasions the buds appear always to possess the power of selecting the most convenient points of origin. The majority of leaf-axils are altogether destitute of buds, and it is only at spots where their inception would be most favourable to the plant's development that a few hardy buds are put forth. This is what happens, for example, in most species of Spurge, in the Toad-flax, in Pines and Firs, in Araucarias, and the rest of the numerous family of Conifers. Where buds are formed in the axils of leaves, either there is one to each leaf, or several are crowded together in an axil, and of these one is conspicuous owing to its central position, and also usually for its size, whilst the rest are subordinate. The occurrence on the leafy region of the stem of buds crowded together in this fashion—the meaning of which will be examined in detail in the next few pages—is confined to certain species belonging to the Flora of the Mediterranean, of Australia, and of various Steppe-lands. They are much more commonly found on such regions of the stem as bear scale-leaves, especially in bulbous plants, which sometimes exhibit as many as a dozen little buds springing from the short, thick stem in the axil of one of the expanded scaly leaves of the bulb.

The buds produced in the floral region of the stem (or inflorescence) usually develop into flowers, and their function being the production of fruit, they cannot be considered until a later section of this work is reached. Meanwhile the bud-form of brood-body is not entirely absent from this region of the stem. Grasses, Saxifrages, and Polygonums afford a great number of examples of their occurrence in that position.

A wound may cause the formation of a bud at any altitude upon the stem. The bud invariably springs from the injured spot and often no relation can be detected between its point of insertion and the position of the leaves. An instance is known where the herbaceous stem of a Sea-Kale (*Crambe maritima*) was cut through transversely, and, after the pith had decayed, buds were formed on the inner surface of the vascular-bundle ring from the tissue of the so-called vascular-bundle sheath, and from the buds shoots eventually developed. If the main trunk or a branch of an Angiospermous tree, such as an Oak or Ash, is cut off smooth, a mass of tissue is formed from the cambium, thus exposed, at the boundary between wood and bast; this tissue gradually creeps out from the margins of the wound and swelling up takes on the form of a circular rampart. The wood-cells which have been cut through and left bare within the circumference of the rampart have not the power of dividing and multiplying so as to initiate a new structure, but are dried up by exposure to the air and perish. The tissue forming the rampart continues, however, to increase in breadth, and encroaches upon the dead interior of the section of the stump so completely that the cut surface of wood

is quite covered over by the new growth. The latter is termed "callus", and may be compared to the tissue which is developed when an arm or a foot is amputated, and which grows from the ligaments beneath the skin until it gradually covers the whole stump. The callus in plants derives a special interest from the fact that within it are formed the rudiments of fresh buds, from which subsequently spring the shoots which "break" so plentifully. A longitudinal section through an Oak stump thus overgrown shows the callus wedged, as it were, between the old bast and the old wood; and we find that it consists of cork and parenchymatous cells, whilst vascular tissues, springing from the wedged portion of the callus, have also been developed, and, descending in bent and tortuous lines, establish an organic connection with the old trunk. The buds arising in the callus do not stand in any relation of any sort to the leaves, as has already been mentioned; nor do the intervals between them follow a geometric law, as is the case with the buds which take their rise from the axils of leaves. They are for the most part in aggregations and are produced anything but simultaneously. A callus of the kind may continue to produce buds at appropriate spots year after year, and shoots of many different ages may be seen springing from it. One cannot contemplate such a callus growth, covering a stump and sending out shoots as direct off-shoots of the decapitated trunk, without being involuntarily reminded of trees that have been "ennobled" by grafting in the manner described in vol. i. pp. 213, 214. There is also an analogy to certain parasitic plants, such as *Loranthus*, in which the connection with the host is established in exactly the same way as that between callus-buds and tree-stump by means of a tissue interposed between wood and bark (*cf.* vol. i. p. 211).

A formation of callus ensues upon the excision of the cortex from the side of a stem in the same manner as when the entire trunk is sawn through; and the process of covering up the exposed wood with callus, derived from the tissue lying between the bark and the wood, goes on similarly in the case of lateral injuries to the trunk. Some trees in addition exhibit a formation of callus without external damage having been received, as, for instance, the Ash, which has a bark liable to split and break open here and there spontaneously, whereupon a tissue of the nature of callus is formed in the open places. Oldish trunks of the North-American Ash (*Fraxinus nana*) are invariably covered with swellings and callosities of the kind, and most of them furnish starting-points for a score or more of buds.

The buds which spring from growths of callus on trunks must not be confounded with those called by foresters "dormant eyes" and "dormant buds". Nor must we fail to distinguish them from the structures which have been termed superposed and collateral buds, which whilst exhibiting extreme diversity in their various modes of development, yet all constitute contrivances for the preservation of the plants from destruction in that their function is to replace dead shoots. With reference to the part played by these structures, it is most convenient to classify them under the name of "reserve-buds". They either originate simultaneously with those which they are destined in certain circumstances to replace, or they

are only subsequently formed in the cortex in the immediate neighbourhood of the points of origin of shoots which have already withered. The latter is of comparatively rare occurrence. In *Spartium scoparium*, which is represented in vol. i. p. 331, one bud only is produced in each axil. The following year, this bud grows out into a long switch, and at the same time a new bud is initiated in the cortical tissue just beneath the base of this shoot. If the first shoot dies next year, as often happens, especially in the case of plants growing near the northern limit of the Mediterranean region, the second bud produces a shoot, and close under its base is formed once more the rudiment of a bud for future substitution. This may go on for several years until at last a whole row of withered stumps are to be seen above the last substituted shoot. This mode of growth, which has been observed not only in *Spartium*, but also in several allied Papilionaceæ belonging to the Mediterranean Flora, is very prejudicial to the freshness and vigour of the plant's appearance. The presence of a number of withered remnants crowded together produces an impression of disease and starvation; else, as an alternative, one is tempted to suppose that the bushes have been cropped by cattle, or annually truncated by man, whereas they themselves accomplish all these changes without any damage of the kind being inflicted.

In *Robinia Pseudacacia*, the plant known by the name of Acacia, a single bud is formed at first in the axil of each foliage-leaf. But later on the stem close to the thickened base of the petiole becomes hollowed out, and in the cavity thus formed little knobs arise underneath the first bud. Sometimes there is one only, sometimes there are two or even three. These knobs are nothing more or less than first rudiments of reserve-buds which develop in this position where they are sheltered and protected by the remaining portion of the petiole. If, as is often the case, in the following year the shoot put forth by the first bud dies, it falls to the uppermost reserve-bud to develop into a substitution-shoot, which may perish in its turn and be replaced by the next reserve-bud. The different species of the genus *Gleditschia* behave in precisely the same way as *Robinia Pseudacacia*, but in them the reserve-buds are only partially hidden beneath the remnant of petiole, and the power of forming new buds at the ends of the branches is here almost unlimited. In some species of *Gleditschia*, e.g. *G. Caspica*, a substitution of shoots, one for another, as they successively dry up, takes place for a period of ten or more years. The consequence is that the long branches of these trees are nodulated at the seats of origin of the buds, and the dried stumps of upwards of twenty short branches dating from previous years are seen crowded close together on these nodes.

In *Pterocarya Caucasica*, a Caucasian tree allied to the Walnut, a single bud is formed every year in the axil of each foliage-leaf, and this bud has the peculiarity of being elevated from 1·5 cm. to 2 cm. above the leaf-insertion. Whilst it is growing next year into a shoot, the rudiment of a reserve-bud is formed just above the original leaf-insertion, but it only develops in some subsequent year in the event of injury to the first shoot.

Far more common than the above are the cases where the buds which sprout in

the first year and those which remain dormant until called upon to replace the earlier ones originate all together simultaneously. In the Common Elder (*Sambucus nigra*) two buds are formed one above the other in each leaf-axil; in the blue-berried Honeysuckle (*Lonicera cærulea*) and in several of its allied species, three buds of almost equal size are superimposed one above another in a straight line in each axil. In the year following their formation, usually only one of them grows out into a shoot; the others stop as they are, and maintain their vitality for a couple of years in reserve and only then develop if the first shoot has met with destruction. The North-American False Indigo, species of which (*e.g. Amorpha fruticosa, A. glauca,* and *A. nana*) are cultivated as ornamental shrubs in European gardens, produces two buds of different sizes above each foliage-leaf, the larger of the two being placed just above the smaller. The former sends forth a shoot in the following year, the latter remains in reserve. If the shoot first developed withers, as very often happens, the reserve-bud sprouts, and the withered stump of the first shoot is then visible just above the fresh one. The North-American tree *Gymnocladus Canadensis* also exhibits on the upper ramifications of its powerful branches two superimposed buds above the insertion of each leaf; the larger is situated above the smaller, and the latter only develops into a shoot in the event of its being required as a substitute. Several other woody plants which, though their stems become very thick, possess neither the growth of a tree nor a symmetrical crown of foliage—such as the Judas-tree (*Cercis Siliquastrum*) and the *Forsythia viridissima* of Japan—put forth long switch-like shoots, the upper halves of which often die off during the winter. The buds on the lower surviving half of each shoot are very close together, and generally they are in pairs, the upper one in each pair being close upon the lower. Only the upper one of a pair is at first developed in the next year; the lower bud does not develop unless the other fails.

It is sometimes the case that the axil of every leaf produces three buds set side by side instead of one above another. The middle bud sends out a shoot in the following year whilst the lateral ones are left as a reserve. The year after, if the shoot has died, what happens is either that one of the two accessory buds develops—as, for example, in *Lonicera fragrantissima* and in the case of the long shoots of the Nettle-trees (*Celtis Tournefortii, C. orientalis, C. occidentalis*), or both accessory buds develop simultaneously—as in the Southern Reed (*Arundo Donax*) and in several species of the genus *Bambusa*. The species belonging to the genus *Xanthoxylon* form in each leaf-axil the rudiments of from nine to eighteen buds, of which the middle one is the biggest and grows out during the following year into a short or long shoot. The other smaller buds are kept in reserve in the cortex at the base of the shoot.

In the Tree of Chastity (*Vitex Agnus-castus*) four buds are set in the axil of each foliage-leaf. The central bud is the largest and a smaller one is situated underneath it, whilst the other two—also smaller—are posted to the right and left respectively of the first. Next year a shoot is put forth from the large central bud whilst

the other three remain dormant. By the second year this shoot has probably perished, and in that case the little reserve-buds sprout. Their development is not infrequently simultaneous, so that here and there upon the tree we have tufts, each consisting of four slender shoots—one withered and three green—which all radiate from one point. If the three later shoots dry off at the ends, the buds on their basal parts produce fresh shoots, and the bushes present a bristly and not very ornamental appearance like besoms, especially when they are destitute of foliage.

A curious development of reserve-buds may also be observed in *Atraphaxis*, a ragged shrub indigenous to the Steppes of Southern Russia. Four buds are formed simultaneously and in close proximity to one another in the axil of every foliage-leaf. Of these a very small one is immediately above the insertion of the leaf; it has a large one above, and two of medium size on either side of it. The large bud becomes a leafy shoot and the small one a blossom. The two lateral buds are kept in reserve unchanged during the second year, and in some circumstances during the third also. If the shoot dies, the development of the lateral reserve-buds is proceeded with; but as soon as they begin to sprout, the rudiments of fresh reserve-buds are formed in the cortex to the right and left of those that are thus developing. Here again, the ragged habit of growth of the shrub is connected with its peculiar mode of bud-formation. The following case is also very common. Of a crowd of axillary buds, placed either side by side or one upon another, one or more produce flowering shoots. When the fruits generated in the flowers have dropped—an event in this connection equivalent to the fall of the shoots which bear them—and the spots of detachment are scarred over, the reserve-buds come into play for the first time. In *Spiræa crenata* there is only one such reserve-bud; in the Dwarf Almond (*Amygdalus nana*) and the Mahaleb (*Prunus Mahaleb*) there are two or three. The diversity amongst plants in this respect is almost endless, but the compass of this work does not admit of the subject being treated in greater detail. Seeing, however, that the facts involved have not received due consideration on the part of botanists, I should like to draw attention to the peculiar phenomena of development in *Buddleia*, *Rhodotypus*, *Fontanesia*, *Philadelphus*, *Rubus*, *Berberis*, *Caragana*, *Alhagi*, *Lycium*, and *Ephedra*, and also to point out that amongst woody, shrubby and suffruticose Steppe-plants, which are especially liable to frost-bite and desiccation, many exhibit highly interesting characteristics in their development of reserve-buds.

In Willows we find a form of reserve-bud which differs from all the rest. It is obvious at a glance that every bud on an annual shoot of a Willow is entirely shrouded by a single scale shaped like a hood. This bud-scale originates in the outer layers of the cortical tissue, and is, so to speak, a raised piece of the cortex covering the rudimentary bud. The large bud wrapped in this scale possesses an axis which has arisen laterally from the axis of the branch which bears the bud, and the vessels and cells of the wood may be followed uninterruptedly from the branch to the base of the bud. But, close to the latter, we also notice some very small bud-rudiments with no bundles running into them from the branch. They take their

rise in a special cellular tissue intercalated in the cortex, and on a branch in its first year are not externally visible, because they are covered by the large hood-shaped scale. The tissue of cells from which these small buds spring might be compared to a callus if it were not produced on wholly uninjured branches and long before the formation of cracks and fissures in the bark. In the second year, when the large central bud begins to produce a lateral branch, throwing off the hood-scale and elongating its axis, the small buds also become visible in the form of spherical or oval knobs at the base of the new side-branch springing from the large bud. They do not, however, get larger or smaller, but remain completely dormant and unaltered. There is even a possibility of their never developing further, but in the event of the branch at the base of which they were produced receiving an injury and dying, they are aroused from their lethargy and grow out into leafy ramifications. It is obviously their function to replace such of their predecessors as fall victims to unfavourable external conditions.

The Crack-Willows derive their name from the extraordinary fragility of their branches. The hard bast and wood at the base of their one-year-old and two-year-old branches exhibit a peculiar structure, the result of which is that a slight shock is sufficient to sever the tissue, so that the branch breaks across at its base and drops off. It seems to be an advantage for these Crack-Willows to get rid of certain leafless and useless twigs which bear nothing but the scars of shed catkins, and are merely an encumbrance. Thus much is certain, that several kinds of Crack-Willow cast off spontaneously a number of these branches, and that the buds above described as lying dormant in the cortex put forth leafy shoots as substitutes. Similar phenomena may be observed in Poplars. But in them the twigs break off at a little distance from the base, and the substitution of green, leafy branches for those covered with dead excrescences is effected by means of reserve-buds preformed in the axils of former bud-scales. There can be no question of mutilation in these cases any more than in the autumnal shedding of leaves which takes place spontaneously for the benefit of the plants concerned, and is not susceptible to the influence of external conditions except inasmuch as the latter may accelerate or retard it.

In all the cases hitherto described, the substitution-buds are developed in the cortical tissue. At first, there is no direct connection between them and the woody tissue of the stem; it is only when these buds are roused from their lethargy, and called upon to put forth shoots, to replace anterior or collateral shoots which have fallen, that communication with the wood, and to that extent also with the current of crude sap, is set up by means of special conductive strands.

There is, however, another form of accessory bud, which is connected from the very beginning with the wood of the stem appertaining to it, and maintains this during its whole life. In forestry the name of "dormant eye" already referred to is employed in particular for this form of bud. If a year-old branch is examined, it is found that the buds in the leaf-axils of its upper half are strikingly larger and more vigorous than those near the base; indeed, above the point of insertion of the

lowest scale-leaves of the branch, it is not even possible in most cases to detect so much as a swelling that might be construed into the rudiment of a new bud. It is not till a longitudinal section is made through the lowest part of the branch that one perceives the existence of buds, here, too, in a very rudimentary condition and buried in the cortical tissue. The large buds to be seen at the close of the first year about the middle and at the extremity of the branch develop next year into fresh branches, the lower parts of which are again clothed with bud-scales, and the upper parts with foliage-leaves; but the small, inconspicuous or invisible buds at the base of the first year's shoot are left undeveloped and completely dormant. They are preserved practically unaltered in size or shape at the spots where they originated within the cortex, in some cases showing above the surface, in others concealed by the outer coats of the bark; and the only change which takes place is that the bundles leading from the wood of the branch to the dormant buds elongate yearly to the extent of the thickness of the new woody ring. These bundles exhibit the same disposition as those within the shoots which are visible on the surface, and so far, we might look upon them as latent lateral axes or side branches imbedded in the wood of the main branch and terminating in dormant buds. The analogy is confirmed by the fact that the lateral axes buried in the wood are capable of ramifying in the same manner as those which project beyond the periphery of the stem and send their branches out into the air. The rudiments of fresh buds may also be formed on the concealed branchlets within the wood of the continually thickening main axis; and in many trees densely-branched structures terminating in dormant buds are formed in the wood of the stem, and exercise a disturbing influence on the course of the surrounding tubes and fibres of the wood of the main stem, causing them to bend and twist about to a very great extent. In this manner knobs of various sizes are formed, composed of the branched latent shoots which terminate in dormant buds and of winding wood-fibres. These nodules are found interspersed amongst the elements of the wood, which pursue a normal course, and they are known as "bird's eyes". Sections of such bird's-eye timber were much in demand some decades ago for use as veneering in cabinet-making, owing to the curious traceries exhibited by them, which usually take the form of eyes surrounded by rings and of serpentine lines—the former corresponding to latent branches, the latter to sinuous wood-fibres.

As already mentioned, in many trees and shrubs it is particularly the buds pertaining to the axils of the lowest leaf-structures that are kept back in a dormant condition. A striking deviation from this habit is exhibited by the Tamarisks (*Tamarix*). The young branches, covered with innumerable little leaves and an assemblage of buds—usually three in number—are formed in the axil of each leaf. Want of space would of itself be sufficient to make it impossible that all these buds should produce shoots in the following year and develop simultaneously; about a thousand lateral branches would in that case be produced simultaneously from an axis little over a metre in length. As a matter of fact only comparatively few of the buds produce shoots, and these are so aptly distributed that no one of them

restricts the freedom of another by pushing it aside or competing for its supply of air and light. Hundreds of rudimentary buds, not only at the base but scattered over the entire length of the branch, remain dormant in the Tamarisk branch, as it grows thicker and thicker, and thus is explained the fact that shoots springing from such branches have an almost inexhaustible store of lateral shoots, and are capable of producing every year afterwards hundreds of fresh shoots.

Those reserve-buds which are formed in the cortical tissue and have no connection with the wood of the stem which bears them, for the most part maintain their vitality only for a few years. The dormant buds at the extremities of latent branches may, on the other hand, preserve their capacity for development for many years, although they undergo no change either in shape or in size. No doubt many of them die in the course of a year or two without being replaced by others; whilst many others which perish have their places filled by new ones developed at the ends of embedded branches. But these are rare occurrences in comparison with the large number of cases where dormant buds retain their vitality for many years.

Suppose the case of a tree one hundred years old, which has been shattered by a violent storm. With its crown of foliage torn down and its great branches broken off and strewn upon the ground, it reminds one of the ruins of a building of which roof, gables, battlements, and walls have been partially demolished. Where previously thousands of leafy boughs formed a spreading crown, now a few riven stumps are seen standing in dreary solitude. The tree has the appearance of being hopelessly destroyed, and one would anticipate that its trunk would dry up completely in the following year. Yet, marvellous to relate, fresh life quickens in the old and shattered trunk. Buds which have lain dormant in the cortex during scores of years stretch out, push their way through the fissures in the bark and develop into vigorous branches, and within a twelvemonth the thick stumps of the old trunk and branches are covered over with a drapery of fresh shoots which have buds set in the axils of their leaves. After another year has passed lateral branches develop from some of these buds, and this process continues until, in about ten years, the maimed tree becomes furnished with a new, densely-ramifying crown of foliage. Who, after witnessing such a phenomenon as this, can doubt that the arrested development of a portion of the cauline buds is an adaptation to ensure trees and shrubs against destruction in case of their being fractured by the wind or otherwise mutilated, or that dormant buds are to be looked upon as a reserve to meet possible accidents in the future!

The fact that twigs which have shed themselves or succumbed to adverse external influences are replaced out of the store of dormant buds or by the buds of the callus, has led to various interferences on the part of man with the natural growth of cultivated plants, and has given rise to a whole series of methods of propagation, which have been employed by farmers and foresters ever since ancient times. To this class of operations belongs, for example, the method employed to promote the growth of underwood, which mainly depends on the development

upon the stumps left when the wood is cut, of new shoots from the callus or from the dormant eyes, shoots which in the course of thirty or forty years replace the old plantation, that is to say, the mass of wood which has been taken away. Pollarding is another instance. Pollard-trees are kept cut down to a particular height, and in consequence become thickened at the top, as may be seen in the case of Poplars, Ashes, and more particularly Willows. The pruning of Vines and Fruit-trees is likewise of this category, and the same process is applied also to the woody plants trained to form espaliers or hedges when a park is being laid down or an estate inclosed. All these manipulations have in view, on the one hand, a development of more vigorous shoots from the stumps that are left behind and the acquisition of as abundant a yield of timber, forage, or fruit as possible; on the other hand, a denser growth of the tree-top, or a stunting of the tree, such as is required for gardens in the old French style, with their formal green walls, obelisks, and marvellous ornamentation. Seeing, however, that each of the various trees and shrubs has peculiarities of its own in relation to the formation of callus and dormant eyes, many different modes of pruning are applied to them. We cannot generalize from one case to all the rest, and it would be a great mistake, for example, to try to pollard Apple-trees like Willows, or to convert Pines into underwood. Climatic conditions must also be taken into account in connection with these intentional mutilations of cultivated plants. To give one instance of their effect, it may be mentioned that vine-pruning in Hungarian vineyards is quite different from the corresponding process employed on the Rhine, whilst the latter again differs from the method practised in Northern Italy, which, in its turn, is not the same as that of Southern Italy. In each locality the kind of treatment most adapted to prevailing climatic conditions has been found out in course of time.

BUDS ON LEAVES.

Hitherto only such buds as are developed on roots or on the various regions of the stem have been dealt with; but an enumeration of these does not nearly exhaust the multiplicity of bud-forms which exist. Buds and shoots may also spring from the tissues of leaves—particularly foliage-leaves. These are termed epiphyllous buds or shoots, and they are classified in several groups according to their places of origin.

Before discussing this classification it is necessary to note carefully that epiphyllous buds must be strictly distinguished from those which occur on the foliage-leaves of *Helwingia* and on the leaf-like cladodes (or phylloclades) of Butcher's-broom, &c. As regards *Helwingia* (see fig. 198) careful investigations prove that certain strands proceed from the leaf-bearing axis to the buds seated upon the leaves. Each of these strands represents a lateral axis, but instead of being free it is bound up (or fused) with the midrib of the leaf from the axil of which it springs. The lateral axis thus adnate to the midrib first abandons its connection with the latter at a spot on the lamina, about a third of its entire

length from the base. It there terminates in a bud, or, if it divides, in several buds, and inasmuch as these are flower-buds, it may be looked upon as a flower-stalk. These buds cannot therefore be said to be epiphyllous, *i.e.* to spring direct from the tissue of a foliage-leaf. In reality each is borne upon a structure of the nature of a stem, only the peduncle, stalk, or axis has partially coalesced with the midrib of a leaf. Willdenow, who was the first to describe it, named the plant, represented in fig. 198, the Butcher's-broom Helwingia (*Helwingia rusciflora*),

Fig. 198.—*Helwingia rusciflora*, with flowers seated upon the foliage-leaves.

because the floral buds here as in the Butcher's-broom (*Ruscus*) were borne by foliaceous structures (*cf.* vol. i. p. 333). The two cases are, however, essentially different. The green leaf-like structures in the Butcher's-broom, which carry floral buds upon their upper surfaces, are not leaves at all, but leaf-like shoots, that is to say axes, and the buds upon them are, therefore, not epiphyllous but cauline. The same statement applies, of course, to other plants with flat, expanded shoots, a few representatives of which are shown in the illustration of p. 335 of the first volume, and in this category must be included Ferns also, if we look upon their fronds as phylloclades, and not as foliage-leaves. It would be quite out of place here to enter into the question of the nature of fern-fronds, or to set forth the reasons why they must be considered as phylloclades. The proof cannot be

conveniently introduced until we come to the description of Ferns themselves. It is sufficient to mention here that buds very frequently occur on the fronds of Ferns; indeed, certain species, *e.g. Asplenium bulbiferum* (see fig. 200) develop buds on almost all their fronds. In most cases they spring from the surface of the green pinnæ, but in *Ceratopteris thalictroides*, a common denizen of swamps in the East Indies, it is from the little stalks of the ultimate green lobes, in

Fig. 199.—Formation of Buds on the apices of the Fronds of Ferns: *Asplenium Edgeworthii*.

Gleichenia from the angles of the forkings of the fronds (*cf.* fig. 189 [6]), and in *Asplenium Edgeworthii* (see fig. 199), from the apices of the fronds, that is to say from the extremities of the cladodes. The last-mentioned Fern grows upon the bark of trees, and the tips of its fronds are endowed with the property of avoiding the light, in other words, they bend towards the darkest parts of their substratum, creeping into the fissures in the bark, where they become firmly adnate, and each develops a bud above the point of contact. This bud gives rise once more to fronds, of which, however, one only, as a rule, develops vigorously. After it has unrolled itself, this new frond in turn searches with its apex for a dark rift. The

process is repeated over and over again, and results in the trees, upon the bark of which the *Asplenium* has established itself, being regularly encircled and woven over by fronds, as is shown in fig. 199. The separate fronds of the fern in such circumstances have a strong resemblance to the runners of certain species of *Veronica*, *Ajuga*, and Periwinkle, which have their leaves arranged in two rows.

Unlike the above cases—viz. the buds of Helwingia borne on special stalks adherent to the leaves, those growing on the cladodes of the Butcher's-broom, and those on the fronds of Ferns, all of which must, in spite of their extreme similarity to epiphyllous buds, be looked upon as cauline—true epiphyllous buds always arise from cells of a true leaf and have no connection with adjacent axes beyond that involved in the fact of the bud-producing leaf being derived like all other leaves from a stem. Epiphyllous buds are even produced by leaves severed from the axis; indeed, in many instances, the severance of the leaves is itself the apparent cause of the development of the buds. This phenomenon is exhibited, for example, by *Bryophyllum calicinum*, a plant of the House-leek family which belongs to the tropical parts of the Old World, but has long been cultivated in our greenhouses and has attained a certain celebrity even in non-scientific circles, owing to the fact that Goethe interested himself in it and mentions it repeatedly in his writings. The foliage-leaves of this *Bryophyllum* (see fig. 200 [3]) are deeply divided, the separate lobes being oblong-obovate and conspicuously notched. Every full-sized leaf exhibits in each notch of the margin a group of cells, which is perceptible as a dot to the naked eye. So long as the leaf remains upon the stem there is usually no further development of these cell-aggregates, but if the leaf is plucked off and laid on the earth an active process of division is set up in them, the result of which is the formation of a little plant with stem, leaves, and roots, as is represented in the figure opposite. The leaves of *Bryophyllum calicinum* are thick and fleshy, and contain when mature such an abundance of reserve material and water as to render it superfluous that any absorption of nutriment from the environment should take place. It is not till later that the little plants which spring from the notches of the leaf, having used up the materials stored in the latter, are driven to seek food from the environment by means of their roots. If the leaf has been laid on moderately damp earth, the rootlets of the young plants, developed in its notches, penetrate the ground and, in the event of the tissue of the leaf being in the meantime exhausted and withered, all the little plants become independent and develop into full-sized individuals. Phenomena similar to those exhibited by *Bryophyllum calicinum* are also observed in other plants with thick, fleshy leaves, particularly in Echeverias. Young plants also make their appearance sometimes on the fleshy leaves of *Rochea falcata* after they have been picked. There is, it is true, the noteworthy difference that the phenomenon is not foreshadowed, as in *Bryophyllum*, by the existence of special groups of cells at the points of origin; but *Bryophyllum*, *Echeveria*, and *Rochea* have this in common, that in all cases the need of materials for the construction of the young plants is met

by the succulent leaf for some time after its severance from the stem, so that it is not necessary to place the leaf in communication with damp earth with a view to its deriving the requisite water therefrom. They are thus exempted from conditions to which the greater number of plants propagated by gardeners by means of so-called leaf-cuttings are subject.

This method of propagation by leaf-cuttings has long been recognized, and has been particularly applied to Citron and Orange trees. as also to the Wax

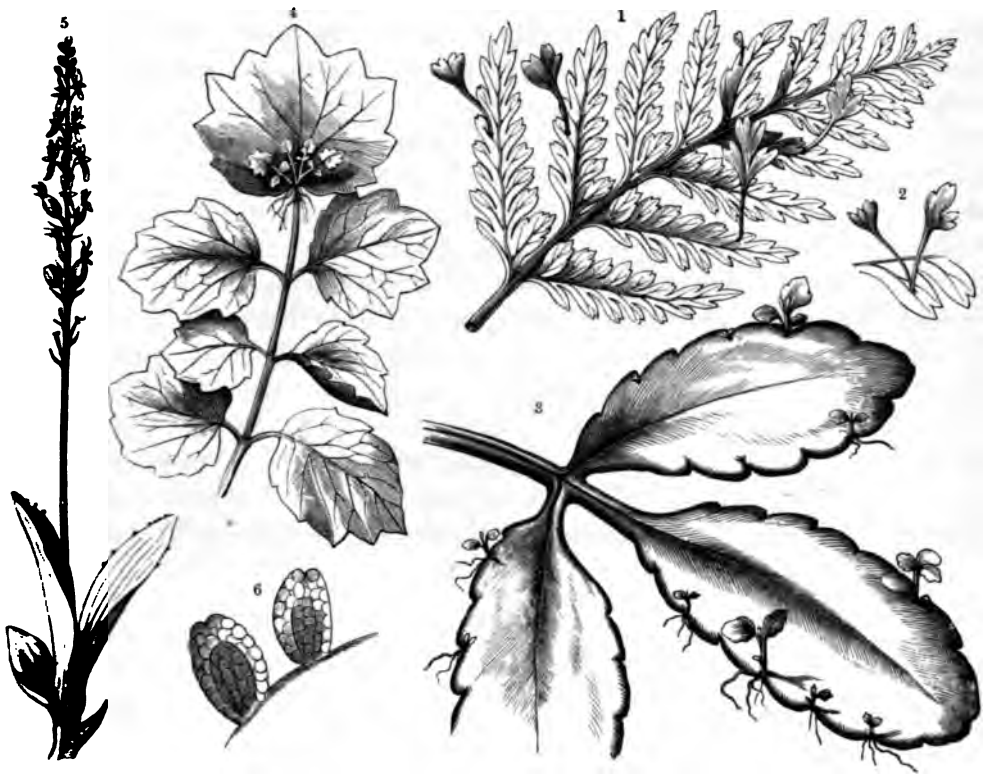

Fig. 200.—Formation of Buds on Fronds and Foliage-leaves:

1, 2 on the pinnules of *Asplenium bulbiferum*; 3 on the margins of the lobes of the leaves of *Bryophyllum calicinum*; 4 on the foliage-leaves of *Cardamine pratensis*; 5 on the margin of foliage-leaves of *Malaxis paludosa*. 6 Two buds on the margin of a leaf of *Malaxis paludosa*. 1, 3, 4, 5 natural size; 2×2; 6×20.

Flower (*Hoya carnosa*), to *Theophrasta Jussieui*, a plant belonging to the Myrsineæ, to the Aucuba Laurel (*Aucuba Japonica*), to the beautiful *Clianthus puniceus*, and to various other plants besides. But it is only quite recently that it has been practised on a vast scale, since the discovery that the Begonias, introduced from the tropical parts of America and now so fashionable as ornamental foliage-plants, and the Gesneraceæ from Brazil with their splendid flowers, are capable of being propagated with extreme facility and in immense numbers by means of their leaves. The cultivator has only to pick one of the foliage-leaves and place it in contact with moist sand or sandy soil, and in a short time

young plants sprout from the leaf and may be transplanted as independent growths. We will briefly describe what takes place.

The first change observed in a leaf which has been cut off for the purpose of forming cuttings is the desiccation of the cells lying next the cut surface. Beneath the layer of dried-up cells a cork-tissue is formed, whilst the dead, outer layer is converted into a bark. A parenchymatous tissue is next formed from the part beneath the cut which is still living; indeed, it is the epidermal cells nearest to the dead layer of cells that initiate this formation of tissue. They grow in a radial direction, elongating and dividing by means of the insertion of transverse walls, the result being a uniform thickening coextensive with the surface of the wound. A little later some of the living cells in the middle of the cut, which are still covered over by the dead layer, begin to divide; and as the tissue there grows in size, it tears the overlying dried layer into shreds and pushes it off in parts. This exuberant tissue has received the name of callus. Whilst the formation of callus is proceeding, suckers are developed at the points of contact of the leaf-cutting with the sand, their numbers being particularly abundant along the projecting ribs of the leaf. In form and function these suckers are entirely similar to the absorbent cells lying close to the growing extremities of roots, and called root-hairs. They are of the greatest importance to the leaf-cuttings in their subsequent processes of development. So long as the leaf adhered to the axis it was supplied with a sufficient quantity of water from that which was ascending through the stem; the aqueous vapour lost through evaporation was replaced by moisture absorbed by the roots from the damp soil and afterwards conducted through the stem to the leaf in question. But when the leaf has been cut off it is no longer able to derive any material from the earth through the intervention of the stem, and as its ordinary epidermal cells have not the power of taking up from the damp soil, which serves as substratum to the leaf-cutting, as much water as is lost by evaporation, the cutting is exposed to the risk of desiccation in spite of its being in contact with a wet substratum. In order to escape this danger and save itself from destruction the leaf treated as a cutting furnishes itself with absorbent cells. By their instrumentality the water, which is particularly needful for the formation of callus, is put by. Even if the materials necessary for the construction of the cells of the callus may be present in abundance in the cells of the leaf, it is of little avail unless these materials are diluted and conducted to the places where they are used up, and for this a much greater quantity of water is requisite than could be retained by the severed leaf. When the callus has reached a certain size numerous roots make their appearance. They usually take their rise from cells of the parenchyma adjacent to a vascular bundle of the leaf, break through the callus, and grow rapidly in length. Only after the development of these roots, which absorb liquid copiously from the substratum by means of their suction-cells, are buds produced on the upper—less frequently also on the under—surface of the leaf-cutting. In Begonias it is chiefly cells of the epidermis

that give rise to buds; in other plants, particularly in the Gesneraceæ, in the species of *Peperomia*, a genus belonging to the Pepper order, in *Tournefortia*, *Citrus*, &c., it is cells of the callus that divide and become the rudiments of buds, and indirectly of shoots. In the case of Begonias isolated buds occasionally spring from the callus in addition to the others, but this is not inconsistent with the fact that in these plants the epidermal cells are the favourite places of inception. Especially are those epidermal cells preferred which are situated above the bifurcation of a vascular bundle in the lamina. If an entirely uninjured leaf is laid upon moist sand, the buds develop just above the base of the lamina where the strands radiate out from one another. It is a common custom of gardeners, however, when making use of Begonia-leaves to propagate the plant, to set the petiole in wet sand and to make a number of transverse cuts across the larger veins of the lamina, which is laid flat upon the sand. After this operation quite a host of buds—*i.e.* new plants—take their rise all along the course of the intersected vein, some immediately in front of the cut, which is covered by a callus, but frequently others again at a distance from that spot. From this we may conclude that the new formation depends principally upon the conduction of material by the veins. No doubt its relative position with regard to the roots developed from the callus to the stock of reserve materials and so forth, also play an important part. The upshot is, however, that numberless cells of the epidermis of the leaf become the seats of inception of new plants, and that buds are able likewise to develop from deeper-lying cells of the callus. Whether the development of an epiphyllous bud has begun in one place or another, there is always in the inceptive area a concomitant production of vascular bundles, which establish a connection between the axis of the bud in process of formation and the previously-developed roots; and it is not long before the axis produces green foliage-leaves capable of assimilating in the presence of light. The leaf-cutting, upon which a miniature plant is now seated, in most cases retains its vitality for a considerable time longer, but at length it begins to turn yellow and gradually it dies. Only that part which produced the buds and roots persists in the form of a pad, forming in some species, for example, in Begonias, a thick, fleshy, cellular body, looking almost like a little tuber.

The phenomenon above described as ensuing in consequence of artificial manipulations takes place sometimes spontaneously in nature in a few plants, and that without the leaf concerned in the process being separated from the axis. Examples of plants which have been observed to bear occasional epiphyllous buds when growing wild in their natural habitats are Cruciferæ (*Cardamine pratensis*, *Nasturtium officinale*, *Roripa palustris*, *Brassica oleracea*, *Arabis pumila*), Papaveraceæ (*Chelidonium majus*), Water-lilies (*Nymphæa guianensis*), Gesneraceae (*Episcia bicolor*, *Chirita sinensis*), Lentibularieæ (*Pinguicula Backeri*), Aroideæ (*Atherurus ternatus*), Orchidaceæ (*Malaxis monophyllos* and *M. paludosa*), Liliaceæ (*Fritillaria*, *Ornithogalum*, *Allium*, *Gagea*, *Hyacinthus*) and Amaryllideæ

(*Curculigo*). In many cases the buds which arise in the form of little papillæ grow straightway into miniature plants, as in the case of the Cuckoo-flower (*Cardamine pratensis*, see fig. 200 [4]), or else little bulbs are formed in the first instance, as in the various species of Garlic and in the Crown-imperial (*Allium* and *Fritillaria*), or small tubers, as in the above specified instances of the genus *Malaxis*. In the one case cells situated in the middle of the lamina—usually above the point of bifurcation of a vascular bundle—are the seat of origin of buds, as, for example, in the Cuckoo-flower, already so often referred to; in other cases, such as *Curculigo*, the buds spring from the extremity of the midrib. The little orchid *Malaxis paludosa* (see fig. 200 [5]), which is a native of moorlands in North-western Europe, develops its diminutive buds principally on the surface and margins of the upper portions of the green foliage-leaves, and these buds appear in such large numbers that several botanists state in their descriptions that the leaves of *Malaxis paludosa* are for the most part "shortly ciliated". Of all the manifold kinds of epiphyllous leaves these little structures produced on the green leaves of the Orchid in question possess a surpassing interest on account of their form. Each bud (two of which are shown in fig. 200 [6]) consists of a yellowish-green cellular body, shaped like a kernel, and of a layer of cells hanging loosely together and enveloping the kernel like a sac. At the free extremity the cells of the envelope form a kind of ring, which constitutes the rim of a round depression. The resemblance of these buds to the seeds of Orchids, especially to those of *Malaxis paludosa*, is obvious on the most cursory examination, and it will again be referred to in a subsequent section.

Buds are found much less frequently on scale-leaves and floral-leaves than on the green foliage-leaves. Sometimes they may be observed to spring from bulb-scales if the latter are stripped off the axis and put into moist sand. In these cases they are invariably developed at the spots where the scales have been cut and injured. Dutch cultivators of bulbs make use of this property to propagate hyacinths direct from the bulb-scales. They cut out the axis of the bulb, remove also any rudiments of floral axis which may be present, and cut transversely through the lower part of the bulb-scales. Not infrequently the bulb-scales are also partially divided longitudinally. One would think that after such treatment the bulb must sooner or later perish; but, on the contrary, a crowd of small bulb-like buds are produced on the scales at the edges of the cuts, and cases are known of over a hundred young bulbs being obtained in the manner described from the scales of a single hyacinth bulb.

Of all epiphyllous buds those originating in the tissue of floral-leaves are, as stated, the least common. Minute buds have, however, been repeatedly observed to be developed, instead of seeds, on the carpels in the interior of the fruits of several species of *Crinum* and *Amaryllis*. They were seated on round bodies of tissue, which were not distinguishable from little tubers. When laid on damp soil, each produced a new plant. We need only allude here to the cases of parthenogenesis, which will be discussed later on, wherein seeds capable of

germinating are developed without fertilization from the ovules concealed in the ovary.

The instances of bud-formation above enumerated, when considered with respect to their origin, show that not only cells of roots, but also those of all regions of the stem, and of scale-, foliage- and floral-leaves may become initial cells of buds, or, in other words, of rudimentary shoots. Hence we may draw the conclusion that all the living protoplasts which are capable of division in whatever part of the plant their cells are situated, from the root-tip to the highest apex of the stem, and from the scale-leaves to the ultimate floral-leaves, have the power of undertaking the function of renovation without previously undergoing fertilization. Under ordinary circumstances, no doubt, it is only protoplasts in the cells of the axis, close to the spots where the foliage-leaves emerge, which turn into rudiments of shoots, and the most natural explanation of the selection of these places is that the constructive materials prepared or temporarily deposited in the foliage-leaves may there be turned to account at first hand; but in extra-ordinary circumstances—*i.e.* as a consequence of unfavourable climatic conditions, or of dangerous injuries, and particularly under the influence of approaching peril of death—the important task of initiating new plants devolves also upon cells situated at most widely different parts of the parent stock, cells which otherwise would certainly not have assumed this function. In these cases it is astonishing to see how stress of external circumstances results in an entirely new division of labour in the cells of the tissue affected thereby; how in one place a protoplast, originally destined to play an altogether different part, divides and becomes the starting-point of a fresh plant, whilst the protoplasts of neighbouring cells convey constructive materials to that particular member of their fraternity and are regularly consumed by it. Very different would have been the order of things and the kind of co-operation of adjoining protoplasts under ordinary conditions!

2. REPRODUCTION BY MEANS OF FRUITS.

Definition and Classification of Fruits.—Fertilization and Fruit-formation in Cryptogams.—The Commencement of the Phanerogamic Fruit.—Stamens.—Pollen.—Arrangements for the Protection of the Pollen.—Dispersion of Pollen by the Wind.—Dispersion of Pollen by Animals.—Allurements of Animals with a view to the Dispersion of Pollen.—The Colours of Flowers considered as a means of attracting Animals.—The Scent of Flowers considered as a means of attracting Animals.—Opening of the Passage to the Interior of the Flower.—Reception of flower-seeking Animals at the entrance to the Flower.—Taking up the Pollen.—Dispersion of the Pollen.—Cross-pollination.—Autogamy.—Fertilization and Fruit-formation in Phanerogams.

DEFINITION AND CLASSIFICATION OF FRUITS.

To all appearance there is no difference between the protoplasts which develop into brood-bodies and those which are the points of origin of fruits. Nevertheless, it has been ascertained by experience that the protoplast, which is the starting-point of a brood-body, evolves its constructive energy without receiving any special stimulus from the protoplasm of a second cell of distinct origin, whereas for the development of a fruit the necessity of such a stimulus is a characteristic and distinctive feature of the phenomenon. Brood-bodies may spring from any part of a plant. If the parent-stock as an individual is in danger of perishing, brood-bodies are developed from protoplasts which otherwise would never have been called upon to play such a part. Brood-bodies may develop on roots, stems, and leaves, on foliaceous prothallia, and on hyphal filaments. They may be formed above or below the ground, and upon or beneath the surface of water. Their origin may be from superficial cells or from cells deeply seated in a tissue. It is scarcely going too far to say that in cell-aggregates of large dimensions the protoplasm of every young cell is potentially the starting-point of a brood-body.

If a fruit is to arise, the *ooplasm*, *i.e.* the protoplasm destined to initiate a new generation, must unite with the fertilizing protoplasm, which is called *spermatoplasm*. The two protoplasts concerned in this phenomenon originate at separate spots, and if they are to coalesce the space between them must be surmounted. One at least of the two protoplasts must accomplish a change of place, and this locomotion must take place in a definite direction. The union of two protoplasts which have been formed at places separated in space from one another constitutes the essence of the process of fertilization, and it results in a change in the ooplasm which, in accordance with our idea of the minute structure of the substances in question, may be looked upon as a displacement of molecules and an alteration in their grouping. Sometimes this internal rearrangement is plainly manifested externally by a change of form and colour, or by an increase in size; and where this occurs it ensues immediately upon fertilization. But for the most part no alteration in the fertilized ooplasm is perceptible at first, and it would be difficult to specify any certain signs whereby the fertilized ooplasm may be distinguished from the unfertilized. It is, however, known by experience that in most cases

the unfertilized ooplasm dies without developing further, whereas the fertilized ooplasm, after a longer or shorter period of rest, exhibits a characteristic growth and becomes the point of origin of a young organism, the new generation. The ooplasm rendered capable, by fertilization, of this particular kind of growth is to be considered as an *embryo*, even in cases where no outwardly-visible change in form, size, or colour has taken place.

Both ooplasm and spermatoplasm are formed in special cells at definite spots on a plant which is preparing to reproduce itself by means of fertilization. The cell-chamber wherein the ooplasm is developed, and which is itself adapted to the reception of foreign matter, and constitutes the point of origin of the embryo, will in future be called an *oogonium* (ᾠόν = egg; γόνος = parentage); the cell wherein the spermatoplasm is brought to the proper form and composition for the purpose of fertilization is called an *antheridium* in the case of a Cryptogam, and a *pollen-grain* in the case of a Phanerogam. In a few instances the ooplasm is set free from the oogonium and fertilized outside it; the oogonium has then, of course, nothing more to do with the subsequent processes of development. In other cases fertilization takes place within the oogonium; the oogonium persists in a more or less altered form as the immediate envelope of the embryo, and is then designated by the name of "carpium" (καρπός = fruit), or briefly "carp". In yet other instances it is possible, at the very earliest stages of development, to distinguish a special multicellular envelope surrounding the oogonium. To this envelope we may apply the term "amphigonium" in order to simplify the terminology. If the amphigonium is later on converted into the coat of the carpium, it may be called an "amphicarpium". In many plants this envelope to the oogonium is succeeded externally by a second called a "pericarpium", which will be the subject of more detailed study later on.

Now what ought we to take to be the fruit? To try to conform to ordinary usage, or to adopt the terms employed in other sciences, would cause fatal confusion. The most expedient course, therefore, seems to be to put aside the names and definitions adopted in other departments and to lay down an independent and unambiguous definition of the plant-fruit, and apply it to all plants. Thus, from the botanical point of view, *we consider every structure to be a fruit which is the product of fertilization, and at the same time constitutes the first step towards the renewal of the fertilized plant.* This definition includes the ooplasm, which is fertilized outside the oogonial envelope, and forms the starting-point of a new individual; there may, therefore, be fruits each consisting of nothing more than an embryo. But usually the ooplasm is enveloped by a coat, which may be single or double, or even threefold. Fertilization then takes place within these coverings, and the influence of the spermatoplasm extends more or less beyond the ooplasm to its investments. In such cases the coats also are involved in the process of fruit-formation. They are stimulated to grow in a particular manner and take the form of a mantle clothing the embryo, of a protective cover, or of some contrivance which promotes the further development of the embryo and its full

expansion into a new generation. Fruits of this kind have sometimes a very complicated structure. In them we are able to distinguish a complex outer coat, and within, the embryo with its tightly adherent covering, the latter portion of the fruit being that which has from ancient times borne the name of *seed*. Fruits thus come before us as a series of forms, of which the members at opposite extremities of the series differ greatly, but are linked together by a large number of intermediate forms. At one end of the chain we have the unicellular fruits of the microscopic Desmids, at the other the fruits of the Cocoa-nut, which is differentiated into seeds on the one hand and several envelopes on the other, and is as large as a man's head.

As already stated, the spermatoplasm acquires the composition and form whereon its fertilizing power depends within the confines of certain special cells. Extreme variety is, however, found to prevail in this connection. In some plants, especially those which conduct the process of fertilization under water, the spermatoplasm takes the form of minute particles usually furnished with special motile cilia to enable them to swim about. These have received the name of *spermatozoids*. They escape from the cell-chambers in which they were formed into the water, rush about for a short time or are carried by currents in the water, and finally reach the ooplasm, whereupon they place themselves in contact with it, and enter into combination with it in a manner which may best be likened to the merging together of two drops of oil floating upon the surface of water. In another category of plants the spermatoplasm does not escape from the cell in which it has been developed, but this cell itself enters into combination with the oogonium as a whole, and a possibility is afforded in a variety of ways for the two kinds of protoplasm to coalesce within a single enveloping cell-membrane. A third category of plants is remarkable for the fact that the spermatoplasm does not coalesce as a whole with the ooplasm, only a portion of it passing to the ooplasm.

The above prefatory remarks give some idea of the extreme variety which exists in the processes of fertilization, and it is no easy matter to give a short and concise, and at the same time accurate, presentation of the facts involved, especially if one tries not to use more than is absolutely necessary the innumerable technical terms invented in recent times. Even taking into account only the most important of the phenomena above referred to, we find twelve different processes or types of fertilization and fruit-formation, and it will be the object of the next chapter to present these in order, beginning with the simplest cases and concluding with the most complicated.

It will materially conduce to clearness of exposition if, in considering these phenomena, we adhere to the old classification into *Cryptogams* and *Phanerogams*, which was introduced by Linnæus. According to the etymology of the words, Cryptogams are plants which are fertilized secretly, whilst in Phanerogams the process of fertilization is apparent. Since the microscope has been perfected and brought into common use this distinction has no doubt lost its significance. If, however, we adopt a somewhat different interpretation of these terms, we may

continue to use them with advantage. Thus, under the name of Cryptogam we shall include all plants destitute of flowers in the ordinary sense and possessing organs of fructification which are not clearly visible excepting under the microscope, whilst the term Phanerogam will comprise such plants as bear flowers, and have organs of fructification which are visible without aid from the microscope and are of the nature of metamorphosed leaves. The retention of these old and familiar terms is rendered all the more desirable by the fact that another important distinction, which is inherent in the process of fertilization itself, and has not as yet received sufficient attention, is involved in the separation of Cryptogams and Phanerogams, namely, that in Cryptogams fertilization takes place in water or in a watery medium, whereas the process in Phanerogams is accomplished almost exclusively in the air.

FERTILIZATION AND FRUIT-FORMATION IN CRYPTOGAMS.

In the mountain districts of Central Europe, after the winter snow has melted and the turbid water derived from it has gradually cleared itself up, a beautiful sight is afforded, especially when a ray of sunshine strikes the water, by the dense crowds of short delicate filaments of a bright emerald-green colour, which everywhere form a coating to the stones at the bottom of streams and to the sides of the troughs used to convey spring-water from the heights. These green threads belong to a plant named *Ulothrix*. Each separate filament consists of numerous cells joined together so as to form a chain, as is shown in fig. 201 [1]. When these filaments are mature, and the time has come for the production of fruit, the protoplasmic contents of the separate cells break up into a number of spherical green masses, which, however, continue to be held together in a rounded cluster by means of a colourless substance. An aperture is now formed in the wall of each of the cells in question, and through this opening the conglomerate mass escapes into the surrounding water (see figs. 201 [2] and 201 [3]). The individual masses of protoplasm which compose the conglomerate are set free shortly afterwards, and each exhibits at its anterior extremity a pair of revolving cilia, by means of which it swims about in the water (fig. 201 [4]). When in the course of their peregrinations two protoplasts which originated in one and the same cell-cavity encounter one another they get out of each other's way; if, on the other hand, the protoplasts from cells belonging to different filaments meet, far from avoiding one another, they come into full collision with their anterior ciliated extremities, turn over, and lay themselves side by side and coalesce, forming a single body with four cilia (see fig. 201 [5]). A little later the cilia vanish, and the product of the coalescence comes to rest. This fusion is the simplest conceivable case of fertilization in the whole realm of plants. The product of fertilization is the fruit. It consists in *Ulothrix* of the little lump of protoplasm formed by the process of coalescence just described, which now surrounds itself with a thick cell-membrane, and fastens on to some stationary body under water (see fig. 201 [6]). We have nothing to do at present with the subsequent development of this fruit; it is

sufficient to remark in order to explain the illustration that the attached unicellular fruit does not produce again immediately a string of cells, but that first of all swarmspores are developed from its protoplasm (see figs. 201[7] and 201[10]), and these fasten on to appropriate spots, inclose themselves in cell membranes, divide and ultimately initiate new filaments composed of cells arranged in linear series as before.

In *Ulothrix* and allied genera the protoplasts which pair as a first step to the formation of fruit do not differ from one another in form, size, colour, or mode of locomotion, and it would be impossible to determine from outward appearances which of them acts as fertilizer and which is fertilized. The terms *ooplast* and

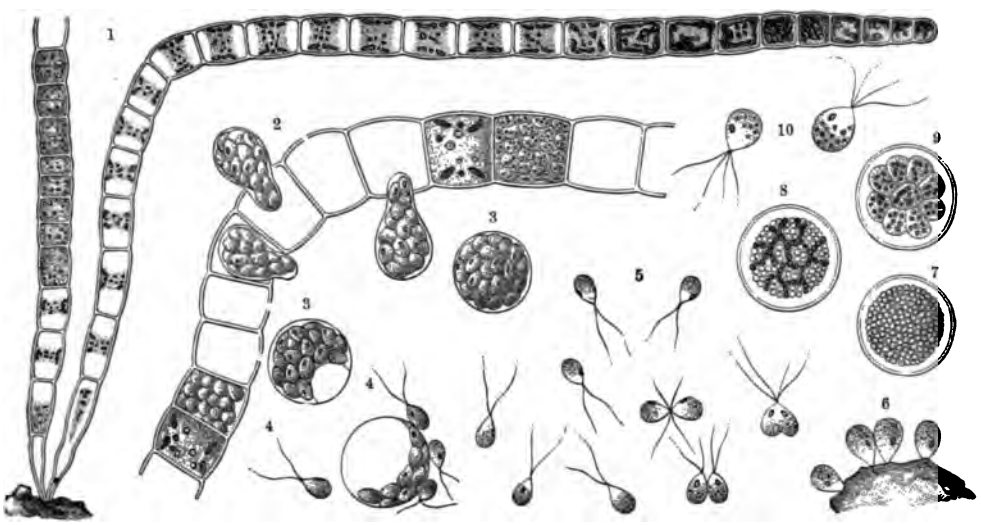

Fig. 201.—Fertilization and fruit-formation in *Ulothrix zonata* (partly after Dodel-Port).

[1] Two filaments composed of cells joined together in chains. [2] Escape of conglomerated gametes. [3] Spherical conglomerate of gametes after it has escaped. [4] Separation of the gametes. [5] Gametes swimming about and pairing. [6] Fruits (products of the pairing of gametes) attached to a substratum. [7–9] Subsequent development of fruit. [10] Two swarmspores produced by fruit. [1] × 250; [2–10] × 400.

spermatoplast are therefore not applied to them, but they are called *gametes*, and the entire process described in connection with them may be spoken of as *fruit-formation by pairing of gametes*. This process of pairing is, so far as it can be apprehended by our senses, a mutual permeation of the two protoplasmic bodies, and we may suppose that a rearrangement of molecules is caused thereby, which endows the product of pairing with the power of developing independently. This assumption is supported in particular by the fact that if any gametes, after being set free from the conglomerate, fail to pair they undergo no subsequent development but deliquesce in the surrounding water and perish.

The Wracks or Fucaceæ, which grow profusely in the sea, resemble *Ulothrix* inasmuch as the protoplasts, destined to act as fertilizers, escape from their cell-cavities, fertilization consisting of a fusion of free protoplasts disconnected from the mother-plant. But these Wracks differ very strikingly from *Ulothrix* and allied forms in that the protoplasts are of two kinds, there being an obvious diversity in

size and form between ooplasts and spermatoplasts. The thallus in all species of *Fucus* is tough and leathery, brown in colour, foliaceous, and dichotomously branched or lobed, and has interspersed here and there air-containing swellings which serve as floats. The apices of the lobes are punctate, and each spot corresponds to an internal cavity which has the form of a globular pit (see fig. 202 [1]). Sections through these cavities show that a large number of segmented filaments known as "paraphyses" spring from the lining-layer of the cavity. In *Fucus vesiculosus* (figs. 202 and 203) these filaments remain concealed in the cavity; in some other species of *Fucus* they protrude through the narrow orifice (ostiole) of the cavity in the form of a pencil of hairs. Amongst the filaments other structures are also formed within the cavity. A few of the cells lining the cavity swell into papillæ, and each becomes divided by the intercalation of a transverse septum into two cells, one of which is spherical, whilst the other assumes the form of a stalk bearing the upper one (see fig. 202 [2]). The protoplasm in the spherical cell is dark brown, and breaks up into eight parts, which round themselves off and constitute the ooplasts. The thick wall of the spherical cell resolves itself into two layers, of which the inner one incloses the eight rounded protoplasmic bodies like a bladder. This bladder stuffed full of ooplasts next detaches itself entirely, and glides upward between the paraphyses until it reaches the orifice of the cavity.

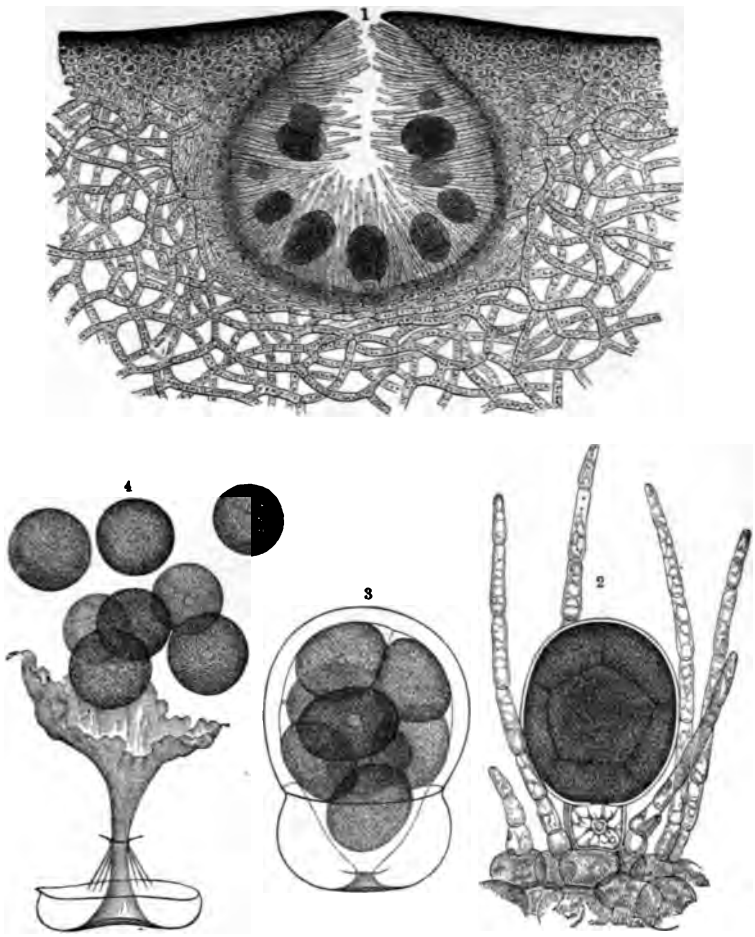

Fig. 202.—*Fucus vesiculosus.*

[1] Longitudinal section through one of the cavities in the thallus. [2] A vesicle surrounded by paraphyses from the bottom of the cavity. [3] A detached vesicle containing eight ooplasts; the inner lamella swollen up. [4] Liberation of the ooplasts from a rent vesicle. (After Thuret.)

Here the bladder splits into two lamellæ, and finally the inner lamella becomes inflated, bursts and shrivels up, leaving the eight ooplasts free (see figs. 202 [3] and 202 [4]).

Whilst a certain proportion of the individual plants of *Fucus vesiculosus* develop ooplasts in the cavities in their lobes, other individuals give rise to spermatozoids in similar cavities (see fig. 203 [1]). The cells lining the hollows develop papillose protuberances which grow longitudinally, divide and form a ramifying mass of cells as is shown in fig. 203 [2]. Here and there the extremities of branches in this mass of cells have a dark brown colour, and their protoplasmic contents are broken up into a number of minute portions (the spermatozoids). These vesicles become detached and collect at the orifice of the cavity. This happens especially at the time when that zone of the sea-shore where the wrack grows is left dry, and the *Fucus* plants are lying flat upon the stones, and look like brown and faded leaves. At the recurrence of high-tide, when the wracks are again submerged, the cells full of spermatozoids burst, and the tiny spermatozoids formed from their protoplasmic contents swarm out into the surrounding water. Each spermatozoid has a sharp and a blunt end, exhibits a so-called eye-spot, and is furnished with two long cilia by means of which it swims about in the water (see fig. 203 [3]). Analogy to similar processes which take place in Mosses makes it seem probable that the ooplasts above described as lying near the orifices of cavities in the thallus secrete some compounds or other—presumably organic acids—which attract the spermatozoids swarming in

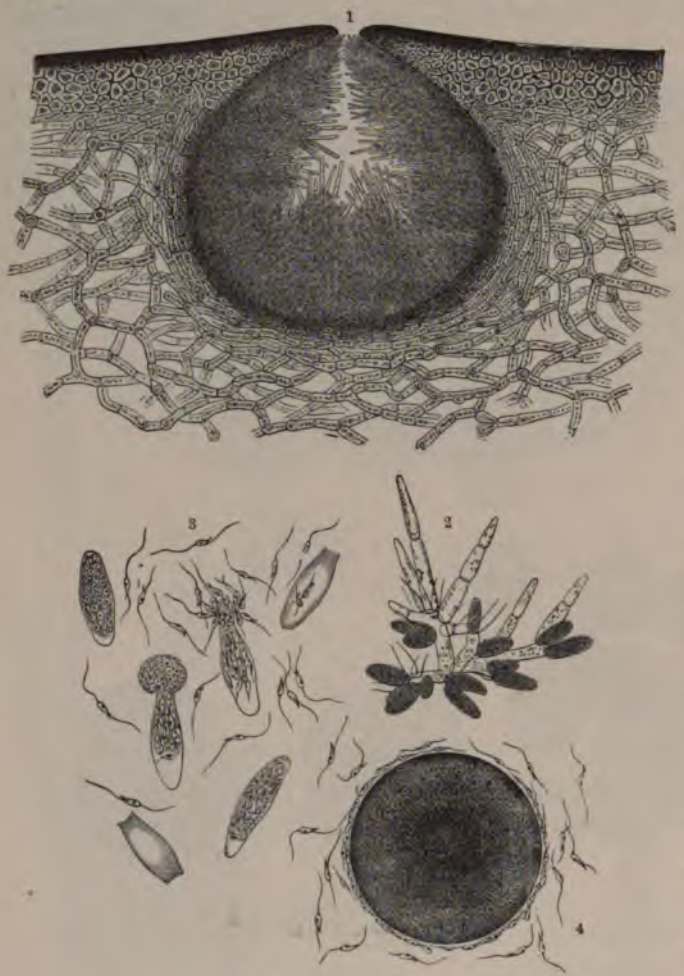

Fig. 203.—*Fucus vesiculosus.*

[1] Longitudinal section through a portion of a thallus including a cavity full of antheridia. [2] Antheridia extracted from a cavity of the kind. [3] Spermatozoids escaping from the antheridia. [4] Spherical ooplast covered with spermatozoids. [1] ×50; [2] ×160; [3], [4] ×350. (After Thuret.)

the water. The actual fact is that spermatozoids which come into the vicinity of the spherical ooplasts adhere to them in such large numbers that a sphere is sometimes entirely coated with spermatozoids (see fig. 203 [4]).

It has also been observed that the spherical ooplasts are set rolling by the adherent spermatozoids, and are thus removed from the places where they previously lay stranded. The fertilizing effect exercised by the spermatozoids, one of

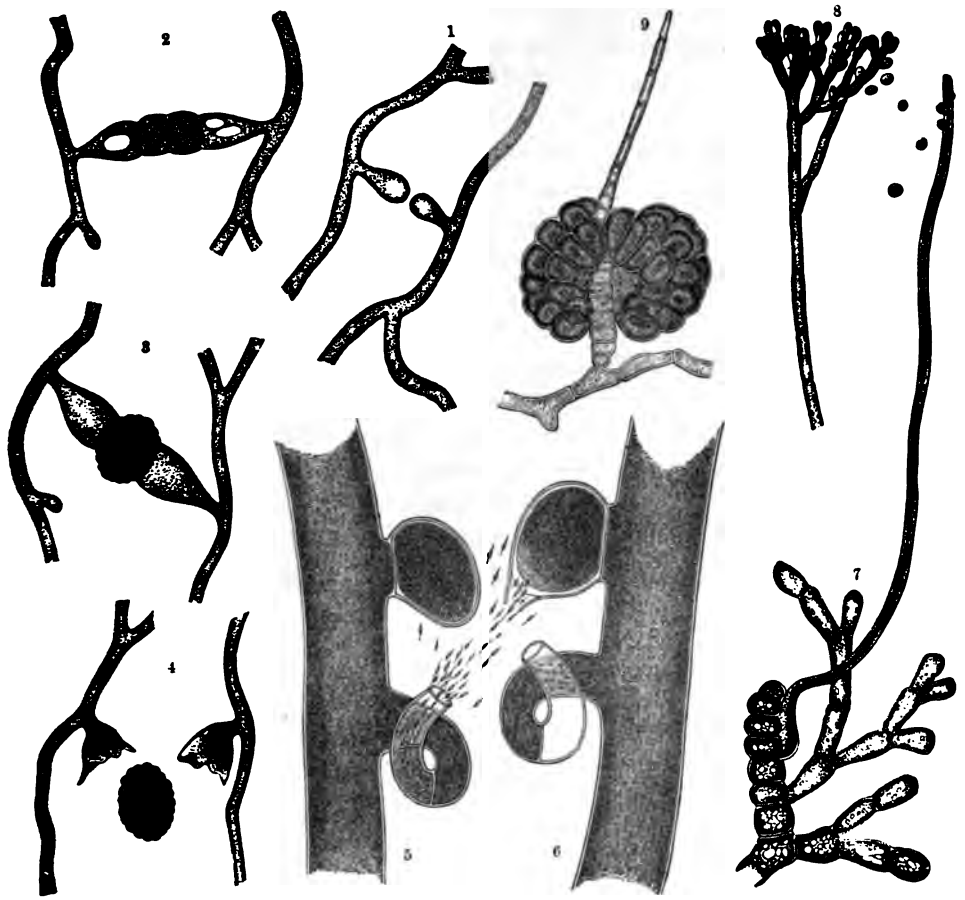

Fig. 204.—Fertilization and Fruit-formation in *Mucorini*, *Siphonaceæ*, and *Florideæ*.

1–4 Conjugation and fruit-formation in *Sporodinia grandis*. 5, 6 *Vaucheria sessilis*. 7 Fruit-rudiment with trichogyne of *Dudresnaya coccinea*. 8 Antheridia of the same plant with spermatozoids in the act of abjunction. 9 Fruit of the same. 1–4 × 120; 5, 6 × 250; 7, 8 × 400; 9 × 250. (7–9 after Bornet.)

which, as it appears, coalesces with the ooplasts, consists doubtless in a rearrangement of molecules, and the first outwardly visible result of this rearrangement is the envelopment of the ooplast in a tough cell-membrane. The body must now be considered to be a fruit—a unicellular fruit, which remains unaltered in a state of rest for some time, but at length bestirs itself, and stretching out attaches itself firmly to the ground by means of root-like outgrowths. It then divides and gradually develops into a fresh *Fucus* plant.

In the two cases just described, the ooplasts are not fertilized till after they have

escaped from the cells of the mother-plants into the surrounding water, and at the time of fertilization they are destitute of any special coverings of their own. In the plants to be dealt with next, on the other hand, the ooplasts at the time of fertilization are still in connection with the mother-plant. The cell-membrane, which maintains this union, persists as an envelope to the protoplasm which is to undergo fertilization. There are two ways in which a fertilizing protoplast may exercise its influence upon a protoplasmic body thus inclosed in a cell-membrane. Either a piece of the envelope is broken through and a free passage made for the spermatoplasm to the ooplasm, or else, if a true fertilization takes place, it must be by osmosis through the envelope.

The solution and removal of part of the cell-membrane enveloping the ooplast, and the opening up of a passage in which the spermatoplast can unite with the ooplast, is observed to occur in the Mould-fungi known as *Mucorini*, and also in the innumerable little green and brown water-plants which, on account of their characteristic mode of fertilization, have received the name of *Conjugatæ*. In these plants the coalescence of the two kinds of protoplasts is always preceded by a process of "conjugation", that is to say, the envelopes surrounding those protoplasts come in contact and grow together, and a special cavity is thereby created in which the fusion of the protoplasts can take place. This method of fertilization is shown in the clearest manner in fig. 204[1,2,3,4], the instance being that of *Sporodinia grandis*, a Fungus belonging to the *Mucorini*. Two more or less parallel tubular hyphæ put forth lateral protuberances (fig. 204[1]) which stretch out towards one another until their free ends come into contact and cohere. As soon as this union is effected, a transverse wall is formed on either side of the plane of contact, and it is now possible to distinguish in the limb connecting the two hyphæ a median pair of cells supported by the two basal portions of the outgrowths (see fig. 204[2]). The connecting limb is usually likened to a yoke (ζυγόν). The wall arising from the junction of the outgrowths, and now separating the two cells in the middle of the yoke, dissolves, thus producing a single cell-cavity (instead of the two), which is called a "zygogonium". The two protoplasts inhabiting the pair of cells were hitherto separated, one being derived from the hypha to the right, and the other from the hypha to the left; they are two different individuals, but, upon the dissolution of the wall between them, they coalesce within the zygogonium. This coalescence is to be looked upon as the act of fertilization. The membrane of the median cell, which surrounds the blended mass of protoplasm, thickens, and, in the selected instance of *Sporodinia grandis*, becomes warted, whilst in *Mucor Mucedo* (fig. 193[3]) it becomes rough and wrinkled, and in other *Mucorini* even spinose. It also acquires a decided dark coloration. Lastly, the dark median cell detaches itself from the basal portions of the original outgrowths, which have held it up to that time, and thus becomes free and independent (see fig. 204[4]). It then drops just as a cherry does from the twig of a tree, and, like the cherry, it must be designated as a fruit, although it consists of a single cell only. Fruits of this kind have received the name of "zygotes".

It is no more possible to say which of the two protoplasts uniting in the zygogonium of *Sporodinia grandis* is fertilized and which acts as fertilizer, than it is to predicate of the pairing protoplasts of *Ulothrix*, that the one is the ooplast, and the other the spermatoplast. Theoretically we must assume there is a difference, and it probably consists in peculiarities of molecular constitution, but no perceptible difference can be detected in size, configuration, or colour, nor is there any apparent distinction in respect of origin.

In the *Desmidiaceæ* also, of which two examples (*Closterium* and *Penium*) are given in vol. i. fig. 25A, *i* and *k*, and in the *Diatomaceæ*, whose species are reckoned by hundreds, no perceptible external difference exists between the protoplasts which unite for the purpose of fertilization. Only in the *Zygnæmaceæ* is it possible to look upon a particular one of the combining protoplasts as an ooplast, and the other as a spermatoplast, and the distinction is in this case founded on their relative positions. An instance of the mode of fertilization prevailing in these plants is well shown in fig. 25A, *l*, in the first volume, the case chosen for illustration being that of *Spirogyra arcta*, which consists of green filaments of a slimy consistence, and occurs very commonly in our ponds. The cells are arranged in linear series, and from some of them are formed lateral outgrowths like those produced by the tubular cells of *Sporodinia grandis*. As in *Sporodinia*, the outgrowths from opposite cells come into contact, coalesce, and form a kind of yoke. Usually a number of the opposite cells of two filaments floating close together in the water establish connecting links of the kind, which resemble the rungs of a ladder (see vol. i. fig. 25A, *l*, to the right). The wall formed by the coalescence of the two apices of the outgrowths is removed by solution, and a channel connecting the opposite cell-chambers of the *Spirogyra*-filaments is thus opened up. In the meantime the protoplasm in each of these cells undergoes a change. Hitherto it has been occupied by a chlorophyll-body in the form of a spiral band, but now it assumes the form of a dark-green spheroidal mass, which is destined to unite with the one opposite to it. In *Spirogyra* this coalescence does not take place in the middle of the connecting canal as in *Mucor* and *Sporodinia*, but the green ball of protoplasm from one cell glides through the transverse passage into the opposite cell-chamber, and there coalesces with the second protoplasmic mass which has remained at rest and not changed its position. It is permissible to call the resting protoplast an ooplast, and the one which moves across to it a spermatoplast; but it must again be expressly stated that in *Spirogyra* no difference in size, shape, or colour can be detected between the two uniting protoplasts. It is worthy of note that the zygote produced by the coalescence, and now assuming an ellipsoidal shape, is not equivalent in bulk to the two protoplasts, as one might expect but that its volume is obviously smaller. We may infer from this that at the moment of coalescence a fundamental change in the molecular structure of the entire mass takes place. The characteristic property of fertilization in the *Conjugatæ*—of which *Sporodinia grandis* and *Spirogyra arcta* have here been chosen as examples—consists in the union of two separate individuals by means of the

formation of a yoke between opposite cells which put forth lateral outgrowths towards one another for the purpose; this is the reason why this kind of fertilization is called conjugation, and the plants concerned are named *Conjugatæ*.

Similar to conjugation, but differing from it in several essential particulars, is the mode of fertilization by means of a protruding outgrowth from the antheridium, which pierces through the wall of the oogonium. This method is observed to occur in particular in the destructive parasites comprised under the name of Peronosporeæ. The species named *Peronospora viticola*, which is represented in fig. 205, has attained a melancholy notoriety as a parasite on the Vine, and to the same group belong *Peronospora infestans*, which causes the Potato-disease, *Cystopus candidus*, known as a deadly parasite on Cruciferous plants, the various species of *Pythium*, &c. Tubular hyphæ develop directly from the spores of these Peronosporeæ, which attack the fresh foliage, green shoots, or young fruits of the particular flowering plants that they select to serve as hosts. The hyphæ bore into the green tissue, piercing through the cell-walls and growing in the intercellular spaces, where they ramify extensively. Segmentation of the hyphæ by the introduction of partition-walls is comparatively rare, but very frequently little suckers, called "haustoria", are sunk into the interior of the living cells of the host (see vol. i. p. 165, fig. 32[1]). These hyphæ infesting the green tissues of the host-plant swell up at their blind extremities into globular heads, and a septum is introduced in each case to partition off the terminal sphere from the rest of the tube, which preserves its cylindrical form. The spherical cell is an oogonium, and the protoplasm forming its contents is the ooplasm. The latter differentiates itself into two portions, namely, a central darker ball and a clearer transparent enveloping mass. The antheridia containing the spermatoplasm develop in the form of lateral clavate outgrowths from another tube, or more rarely from the same tube. These protuberances grow towards the oogonium and apply themselves to its surface. As soon as the antheridium touches the oogonium it sends out from the point of contact a conical or cylindrical hollow process which pierces the wall of the oogonium and penetrates to the dark ball in the middle of the ooplasm (see fig. 205[2]). Meanwhile the protoplasm in the antheridium has differentiated itself into a parietal lining on the one hand and the true spermatoplasm on the other. The antheridial process, which has received the name of "fertilizing-tube", opens at the extremity buried in the interior of the oogonium; within an hour or two the spermatoplasm has flowed through this channel to the ooplasm and become so completely merged with it that it is no longer possible to recognize any boundary between the two. A short time afterwards the fertilized ooplasm incloses itself in a thick cell-membrane composed of several layers. The outermost layer is usually rough and warty, and in some species is even beset with spikes. The fruit thus formed is unicellular and remains so. It frees itself from the now decaying oogonium—thus effecting its separation from the mother-plant—and then enters upon a long period of rest. The new generation developed from the fruit begins as a tube

which subsequently, in some cases, puts out sac-like processes and branches and fashions itself into the likeness of the mother-plant without passing through any intermediate stage; or in others, the tube, which represents the embryo, produces first of all from its protoplasm a number of swarmspores. These roam about for a period and then seek out a convenient spot where they come to rest and develop into new individual plants. The additional production by Peronosporeæ of spores on dendritically-branched hyphæ growing out through the

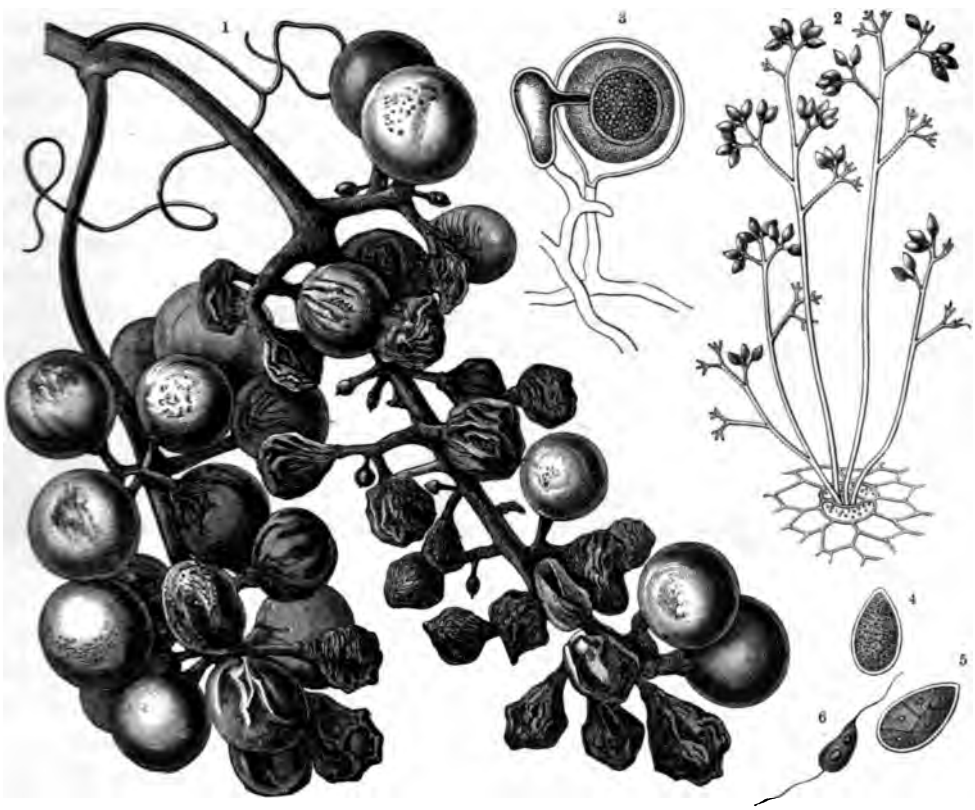

Fig. 205.—Fertilization, fruit-formation, and spore-formation in the Peronosporeæ.

[1] A bunch of grapes attacked by the Vine-Mildew. [2] Spores on branched stalks projecting through a stoma of a Vine-leaf. [3] Fertilization in *Peronospora viticola*. [4] A single spore. [5] A single spore the contents of which are dividing into swarmspores. [6] A single swarmspore. [1] natural size; [2]×80; [3–5]×350; [6]×380. ([3–6] after De Bary.)

stomata of the green host-plants is shown in fig. 205[2], but an opportunity will occur later on of discussing the details of that process.

The Siphonaceæ exhibit a different mode of fertilization from those processes which involve the preliminary construction of a fertilization-tube and a conjugation-canal respectively. All the Siphonaceæ live in water or on damp, periodically submerged earth; they contain chlorophyll and are neither parasites nor saprophytes. We may take as a type of this group of plants, which includes forms of great diversity, a species of the genus *Vaucheria* (see vol. i. figure 25A, *a*, and text p. 23) and use it also to illustrate the processes about to be considered.

If a green filament of *Vaucheria* is examined under the microscope it is found to consist of a single tube without septa, but with numerous saccate branches. The sac-like outgrowths serve a variety of purposes; those at the base fasten the tube to the substratum, those at the free extremity develop swarmspores, whilst those springing laterally from the filament have the functions of fertilization and fruit-formation. The lateral outgrowths are of two kinds (see figs. 204[5] and 204[6]). One form is short, thick, and oval, and usually projects obliquely; the other is a slender cylinder curved like a chamois horn or wound round in a spiral, and sometimes it is subdivided into several little horns. The protoplasm in these sacs severs itself from the protoplasm of the main tube and a partition of cellulose is inserted in the plane of disjunction in each case. We have thus corresponding to each protuberant sac a cell-cavity or receptacle which incloses the protoplasm destined to take part in the formation of fruit. The obliquely-oval receptacles contain ooplasm and are oogonia, the curved, cylindrical receptacles inclose spermatoplasm and are antheridia. Their development is accomplished rather rapidly. It usually commences in the evening, and by the following morning the oogonia and antheridia are already completed. During the course of the forenoon an aperture appears at the apex of the oogonium, whilst simultaneously the ooplasm within it contracts into a sphere. The spermatoplasm in the antheridia has meanwhile broken up into a large number of oblong spermatozoids, with a cilium at each end. After this has happened the free extremity of the antheridium bursts open, and the minute spermatozoids are expelled in a swarm into the surrounding water. Some of them reach a neighbouring oogonium, pass through the opened summit into the interior of the receptacle, and there coalesce with the ooplasm which has contracted into a green sphere. In connection with this phenomenon there is the following very striking circumstance to be noted. Where, as is usually the case, an oogonium and an antheridium are developed in close proximity to one another on the same tube, they seldom open simultaneously, and this circumstance most effectively prevents the fertilization of the ooplast by spermatoplasm of the adjacent antheridium; but on the other hand it usually happens that the spermatoplasm from the antheridium of one tube reaches the oogonium of another tube, and in this manner a crossing of the two takes place (figs. 204[5] and 204[6]).

As soon as an ooplast is fertilized it surrounds itself with a tough cell-membrane; the green colour of the protoplasm changes to a dirty red or brown, and the fruit is to be seen imbedded in the oogonium in the shape of a reddish-brown, unicellular sphere. The oogonium dissolves or else breaks off with the fruit inclosed in it. In either case the product of fertilization is removed from the tube whereon it developed and sinks to the bottom, where it undergoes a comparatively long period of rest often lasting through an entire winter. When the unicellular fruit germinates, the outer layer of the cell-membrane splits, and out of the rent emerges a tube of like form to that which produced the fruit.

In every case of cryptogamic fertilization hitherto discussed a union of the

spermatoplasm with the ooplasm occurs. The protoplasts set aside for the purpose of coalescence forsake the cell-interiors when they have attained to maturity, or at least one of the sexual cells liberates its protoplasm so that it reaches the other unfettered and is enabled to effect a union of their two masses. For this result it is necessary for a part of the cell-membrane enveloping the protoplasm in question to be previously removed, for otherwise it would not be possible to effect the kind of union to which the phrase coalescence of protoplasm is properly applicable. On the other hand, many cases exist in which there is no obvious perforation of the wall, although the changes usually following true fertilization take place. Under these circumstances it is difficult to resist the view that if fertilization (*i.e.* a fusion of protoplasts) really happens (as to which difference of opinion still prevails) it is accomplished by means of osmosis. With this qualification we may say that fertilization by means of osmosis is observed in its simplest form in the Erysipheæ, popularly known as Mildews, in the Moulds allied to *Aspergillus* and *Penicillium*, a description of which in relation to their methods of spore-formation is given on pp. 21, 22, and in several Discomycetes, including the curious Fungus named *Ascobolus*, which will be dealt with more thoroughly when we come to the subject of the mechanisms for dispersing spores.

The Mildew occurring on the surfaces of green foliage-leaves appears under the microscope as a peculiar kind of mycelium. The hyphæ, which are filiform, colourless, and densely interwoven, do not penetrate into the intercellular spaces of the tissue of the host-plant, but satisfy themselves with sinking little suckers into the superficial cells of the leaves and stem (see vol. i. p. 165, fig. 32 [2]). Here and there these hyphal tubes rise erect from the substratum and abstrict moniliform rows of spores; others put forth short, lateral outgrowths which become partitioned off by the insertion of a transverse wall in each, so that the protoplasm in the outgrowth is shut off from the rest of the protoplasm in the tube. Some of these latter structures are oval or club-shaped, and they contain ooplasm and are to be considered as oogonia; the others are cylindrical and sometimes bent into the form of hooks, and they contain the spermatoplasm and constitute antheridia. In a few species the upper, somewhat swollen end of the outgrowth filled with spermatoplasm—*i.e.* the antheridium—bends over the top of the oogonium and attaches itself closely thereto, without, however, sending any special fertilization-tube into the interior of the oogonium; in other Fungi of the Mildew family both cells—the oogonium as well as the antheridium—are spiral and are coiled round one another, and at the same time pressed tightly together. On the assumption that a true fertilization now occurs, this must, as already indicated, be by a diffusion of the spermatoplasm through the cell-membranes to the ooplasm, causing a change in its ultimate structure which corresponds to fertilization. The ooplasm is thereupon converted into an embryo. The cell inclosing the embryo neither dissolves nor severs itself from the parent-hypha, but divides and becomes differentiated into an upper swollen cell and a lower short,

stalk-like cell, and below the stalk fresh tubular outgrowths develop from the hyphal filament in question which become septate and ultimately form a voluminous multicellular envelope round the embryo.

The now mature fruit preserves its connection with the parent-hypha, and is to be seen seated upon it in the form of a minute sphere. When a large number of fruits are developed simultaneously on the hyphal reticulum—as is the case in *Sphærotheca Castagnei*, which is parasitic on the leaves of Hops—the grey mildew spread over the foliage has the appearance of being studded with the tiny globular heads. From the embryo a new generation is produced. In the species of the genus *Podosphæra* it develops, within the cellular mass just referred to as investing the fruit, into a single tube (*ascus*). The protoplasm within the ascus breaks up and fashions itself into true spores, which abandon the tube and are distributed by the wind. In *Erysiphe*, on the other hand, the embryo becomes septate, and takes the form of a simple or branched chain of cells, and it is not till after this stage that tubes are produced whose protoplasm is transformed into a group of spores. The tubes in question are long, erect, and club-shaped, and they spring from the cells of the aforesaid chain.

The manner of fertilization and fruit-formation in *Penicillium*, and generally in all the forms of Mould which are comprised under the name Aspergilleæ, is the same as that described in the case of Mildews (Erysipheæ). In them also the extremities of tubular hyphæ which contain the ooplasm and spermatoplasm, respectively, come into close contact. They are either spirally twisted and wound round one another, or else the extremity corresponding to an antheridium is hooked and grasps the other, as is shown in fig. 193[6] (p. 18). Fertilization takes place by osmosis. The embryo produced by the spiral oogonium is septate and multicellular, and develops club-shaped or egg-shaped outgrowths, whose protoplasm breaks up into round or ellipsoidal balls (fig. 193[7]). This structure becomes surrounded by a continuous multicellular tissue, which owes its origin to the upgrowth of a number of hyphæ from the cells at the base of the oogonium. These hyphæ elongate rapidly, ramify, become intertwined, and develop septa until they constitute a spherical envelope round the embryo. The fruit thus constructed is in *Penicillium* about half a millimetre in diameter.

The Florideæ, or Red Seaweeds, are likewise fertilized by means of osmosis. The details of the process are, however, intrinsically different from those observed in Mildews and in the Moulds classed as Aspergilleæ. The organs developed for the purpose of fertilization have also quite a different form in Florideæ. Their most striking feature is the so-called "trichogyne", a long filamentous cell which projects far above the fruit-rudiment. From this structure the characteristic mode of fertilization in Florideæ is called fertilization by aid of a trichogyne. In some Florideæ the cell containing the ooplasm leads directly into the trichogyne; in others the fruit-rudiment which incloses the ooplasm is septate, that is to say, it consists of a row of broad cells which together form a short branch of the ramifying thallus, and adnate to one side of this row of cells is the long, delicate,

filamentous cell called the trichogyne (fig. 204[7]). Rudimentary fruits of this kind are produced on one individual, whilst antheridia are formed upon another. It is much less common for fruit-rudiments and antheridia to be developed on the same individual, and in the few species which do exhibit this combination, self-fertilization is rendered practically impossible by a retardation of the development either of the fruit-rudiments or of the antheridia. The antheridium always takes the form of a limited portion of the thallus, from which separate round cells filled with spermatoplasm are thrown off. Fig. 204[8] represents an antheridial branch of *Dudresnaya coccinea*. A slender branch of the thallus terminates in a group of cells arranged dichotomously, and the outermost of these cells, which become rounded off and detached, contain the spermatoplasm, and must be looked upon as spermatozoids. Unlike the spermatozoids of *Vaucheria* and those of the Characeæ (Stoneworts), Muscineæ, and Ferns, to be described presently, these have no cilia, and do not move by virtue of any power of their own in the surrounding water, but are carried about by currents which are always more or less prevalent at the places where the Florideæ live. Through the action of these currents in the sea, the spermatozoids (or *spermatia* as they are called) reach one of the trichogynes and adhere to it, as is shown in fig. 204[7]. The question as to how far attractive forces emanating from the ooplasm come into play in order to effect this conjunction must remain undecided. It is not impossible that substances may be secreted by the ooplasm and be given off into the environing water, and that they may take part in the phenomenon. Nothing more definite is known beyond the evident fact that the spermatozoids adhere much more commonly to trichogynes than to other objects floating in the neighbourhood. Part of the protoplasm of the adherent cells passes apparently by osmosis into the protoplasm of the trichogyne. The change ensuing upon this process is transmitted to the protoplasm occupying the ventral enlargement at the base of the trichogyne, and in many cases even further to the protoplasm of adjacent cells. Although this propagation of the change in the molecular structure of the protoplasm cannot be directly observed, it may be assumed on various grounds, and we may fairly suppose that the action of the absorbed constituents of the spermatoplasm upon the ooplasm is comparable to that of certain enzymes, which have a convulsive effect upon any protoplasm in their vicinity, and even when they are separated from it by cell-walls cause a displacement and rearrangement of the molecules (see vol. i. p. 464). That the change affecting the protoplasm at a particular spot in the fruit-rudiment is capable of being propagated so long as any protoplasm susceptible of the same change is present, is proved by the fact that it is not the trichogyne itself but the ventral enlargement at its base and the cells adjacent to this enlarged portion which undergo subsequent development. They increase in bulk, whereas the trichogyne shrivels and dies. The cells which contain the protoplasm fertilized through the intervention of the trichogyne must, in my opinion, be looked upon as the fruit. Any subsequent structure arising from them is no longer fruit but a new generation. In Florideæ, as in so many other cases, this new generation preserves its connection with the

mother-plant, but differs conspicuously in form from the generation from which it sprang. This stage having already been dealt with on p. 22, it is here only necessary to mention briefly that the cells of the fruit begin to shoot out after a period of rest of variable duration and abstrict a mass of spores, and that in addition, in most Florideæ, linear series of cells grow from the cells at the base of the fruit, and form a capsular envelope around the young spores.

The Cryptogams that we have still to deal with, viz.: the Characeæ, Muscineæ, and Vascular Cryptogams, differ from those already described in that the oogonium is wrapped up in a special sheath before fertilization takes place, and that the entrance-passage provided for the spermatoplasm is consequently modified in a characteristic manner. This sheath, to which we shall apply the term *amphigonium* (also known as *archegonium*), is in the main of the same construction in all the plants exhibiting it; but as regards the penetration of the spermatozoids into the amphigonium, and the behaviour of the fruit produced from the fruit-rudiment, there are very considerable differences amongst the groups in question. To follow out these diversities in minute detail is not possible within the narrow limits of this book, and I must content myself in the following pages with giving a brief sketch of the most important phenomena.

To begin with the Stoneworts (Characeæ), we find that in them the fruit-rudiment is ellipsoidal in shape, and is borne on a very short unicellular stalk. This stalk is seated upon the so-called "nodal cell", a short discoid cell which forms the pedestal of the large ellipsoidal oogonium, and also gives rise to five tubular cells arranged in a whorl, and twisted spirally round the oogonium, thus enveloping it in a sheath of great beauty (see fig. 206 [3]). From the ends of these investing tubes, which project above the oogonium, small cells are separated off, and together constitute a little roof for crown to the amphigonium. Beneath the crown the enveloping tubes are drawn together so as to form a neck which incloses a narrow cavity, and this is the part where at the time of fertilization fissures are formed between the otherwise connate tubes of the envelope, thus enabling the spermatozoids to penetrate into the interior of the amphigonium, and to reach the ellipsoidal oogonium there matured.

The mode of genesis of these spermatozoids is extremely remarkable. They are produced in certain red, globular structures, which are slightly smaller than the fruit-rudiments and have a like origin—that is to say, they take their rise amongst the whorls of lateral offshoots. In some species they are formed on the same individuals as the fruit-rudiments (*cf.* figs. 206 [2] and 206 [3]), in others the two kinds of structure develop on different individuals, and are thus separated from one another; hence we distinguish Characeæ into monœcious and dicœcious species. Each red sphere is composed of eight plates, outwardly slightly convex. Each of these is in the shape of a spherical triangle with indented edges and folds running radially from the centre to the notched margins (see fig. 206 [4]). The plates are joined together into a sphere, the notches of the margins fitting into one another so as to form a regular dovetailed suture. From the centre of the gently

concave inner face of each plate a cylindrical or conical cell projects, carrying upon its summit another, capitate, cell. Each of these head-cells is surmounted by long strings of cells, of which the lowest segments are spherical or cylindrical, whilst the rest are short discs (see fig. 206 [5]). The whole structure may be likened to a whip with many thongs, and the stalk-cell projecting from the plate has hence been called the "manubrium" or handle. So long as the eight plates of the sphere are

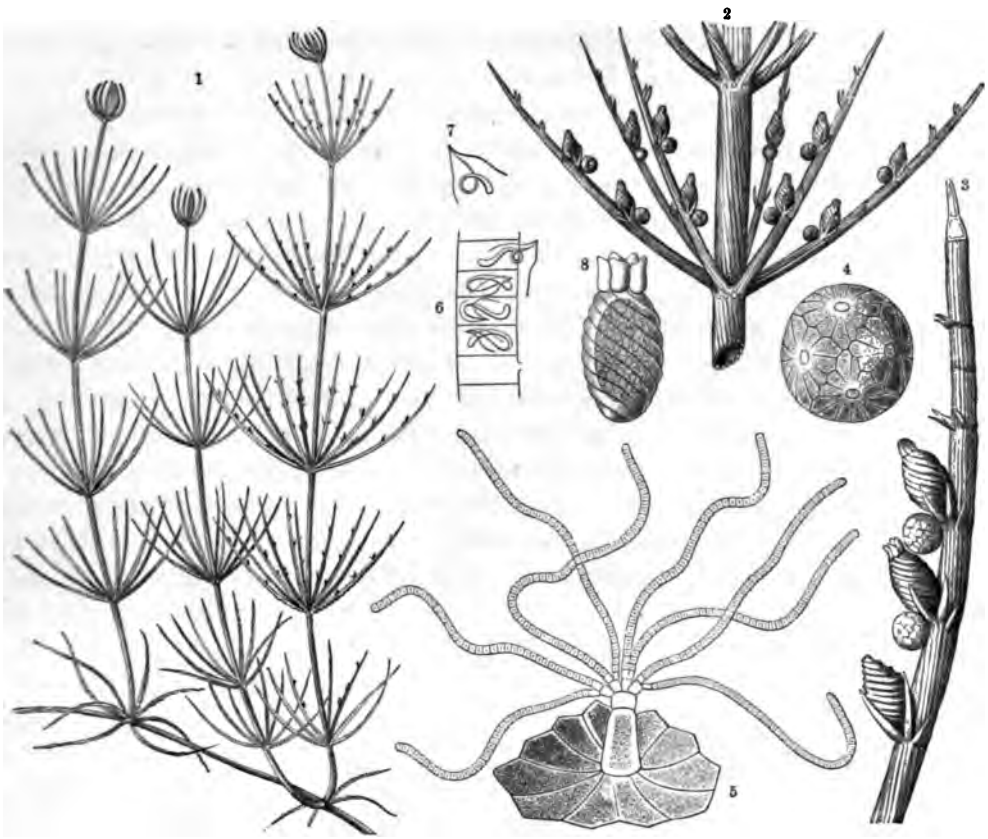

Fig. 206.– Fruit-formation in Stoneworts (Characeæ).

[1] *Chara fragilis*. [2] Piece of the same with amphigonia and antheridia on the branches. [3] A single branch with amphigonia and antheridia. [4] An antheridium. [5] A plate of the antheridium with manubrium and cells grouped in the form of thongs and containing spermatozoids. [6] Several cells from one of the whip-like filaments; the cells in the middle contain each a spermatozoid, the spermatozoid is escaping from the uppermost cell, the lowest cell is already vacated. [7] A single spermatozoid. [8] Amphigonium inclosing the oogonium. [1] natural size; [2] × 10; [3] × 15; [4] × 35; [5] × 100; [6] × 300; [7] × 500; [8] × 50

closed, these manubria project towards the centre of the hollow sphere, and the rows of cells proceeding from the manubria are conglomerated into a ball. But as soon as the plates separate and the sphere falls to pieces, the ball is untwisted and its parts assume the appearance shown in fig. 206 [5]. By this time a spiral spermatozoid has developed from the protoplasm in each of the discoid segments of the filaments, and may be seen lying within its cell (see fig. 206 [6]). But almost immediately afterwards these cells open, and the spermatozoids, which are provided at one end with a pair of long cilia, escape and whirl about in the surrounding

water (see fig. 206 [7]). The spermatozoids then pass through the fissures already described as existing beneath the crown of an amphigonium, and so reach the interior of the latter. Here, in the middle of the cavity is the oogonium (*i.e.* the great cell containing the ooplasm), and over it there is a slimy gelatinous mass, which occupies more particularly the neck of the amphigonium. The cell-membrane of the oogonium is attenuated and almost liquefied, and these soft and swollen masses of mucilage do not interfere in any way with the progressive motion of the spermatozoids. The latter reach the ooplasm, and, so far as we can see, a coalescence of the two kinds of protoplasm takes place.

The changes set up in the fruit-rudiment by fertilization first manifest themselves externally in an alteration in colour. The chlorophyll-bodies, hitherto green, assume a reddish-yellow tint; the spiral cells of the amphigonium become thickened and nearly black, and the amphigonium constitutes a hard shell which acts as an outer envelope inclosing the inner envelope of the fertilized ooplasm, now converted into an embryo. The entire structure next detaches itself from the stalk-cell, sinks under water, and remains for a considerable time—usually through the whole winter — lying unchanged at the bottom of the pond. The embryo does not germinate till the following spring, when it begins by developing a linear series of cells, the so-called pro-embryo, and from one of the cells of this pro-embryo is produced a Stonewort plant with branches in whorls as before (see fig. 206 [1]).

The fruit-rudiment in Muscineæ (Mosses and Liverworts) exhibits in many respects a resemblance to that of a Stonewort, although its origin is quite different. It takes its rise from a superficial cell of the Moss-plant, and the cell belongs, according to the species, either to the foliaceous or to the cauline portion of the thallus. This cell projects in the form of a papilla above the adjoining cells, and becomes partitioned by a transverse wall into an under and an upper cell, the former of which serves as a pedestal to the body of tissue developed from the upper cell. The cellular body referred to is differentiated, by repeated insertion of longitudinal and transverse walls, into a central row of cells and an envelope. Amongst the central cells one situated somewhat low down in the series is conspicuous for its size; it contains the ooplasm, and must be looked upon as an oogonium. The central cells, which are placed in succession above it, are called the canal-cells of the neck. The name is derived from the fact that they occupy the constricted portion or neck of the envelope. The cellular envelope, which incloses the central row of cells and constitutes the amphigonium, is shaped like a flask (see fig. 191 [10]); the lower, enlarged, ventral portion conceals the oogonium, the upper constricted portion is filled up by the neck-cells, and the whole structure, which received from the earlier botanists the name of "archegonium", is closed at the top by a lid composed of several cells. When the time for fertilization arrives the canal-cells of the neck swell up and are converted into mucilage. The lid-cells open and part of the mucilage is forced out; what remains offers no impediment to the admission of the spermatozoids to the ooplasm in the centre of the fruit-rudiment.

The antheridia arise in the same manner as the fruit-rudiments. A superficial cell of the thallus is enlarged into a papilla, and, by the repeated partition in all directions of its first segments, a body of tissue is produced, which includes a delicate stalk and a thickened upper portion, either clavate or spherical in shape. The latter part consists of a multicellular sac-like envelope and a parenchymatous filling-tissue inclosed within the envelope. In each cell of the internal tissue the protoplasm fashions itself into a spirally-bent spermatozoid, and shortly afterwards the entire filling-in tissue is resolved into its separate cells. The antheridium now opens at the top, and the loose cells with the mucilage in which they are embedded are ejected into the surrounding aqueous medium composed of rain or dew-drops. The spermatozoids then escape from their delicate cell-membranes, and swim about the water by the help of the two long cilia wherewith each is furnished (see vol. i. p. 29, figs. 7^{9} and 7^{10}). Passing down the open neck of the amphigonium, now filled with mucilage only, they succeed in reaching the oogonium in the enlarged base of the fruit-rudiment and apply themselves closely to its surface; a constituent portion of the spermatoplasm is absorbed into the ooplasm with the result that the latter becomes fertilized.

Usually several antheridia are situated close together. In Mosses they are mingled with paraphyses, structures resembling hairs, the significance of which has not yet been explained. In many species one individual develops only antheridia, another only amphigonia; but in other species antheridia and amphigonia are developed side by side on the same Moss-plant. Where the latter is the case either the oogonium exhibits an earlier development than the antheridium, or the reverse is the case. Either the passage leading to the oogonium through the neck of the amphigonium is opened whilst the adjacent antheridia are still closed, or else the spermatozoids are set free from the antheridia at a time when access to the oogonium is still barred by the lid-cells of the amphigonium. As in so many cases of a similar kind this contrivance prevents a union between the ooplasm and the spermatoplasm produced by the same individual, and favours cross-fertilization between different individuals.

In some Liverworts the antheridia and amphigonia are surrounded by annular walls, and these organs then appear to be sunk in depressions of the thallus. In other Liverworts separate lobes or branchlets of the thallus are transformed into stalked shields or discs, and the antheridia and amphigonia are formed in special niches and compartments on the surface of the shields. Those Muscineæ which have their thalli differentiated each into a cauline axis and cellular laminæ resembling leaflets, develop antheridia in the axils of the leaflets, or else in pitcher-shaped cavities at the tops of the stems. In Mosses the principal or secondary axes terminate in groups of antheridia or amphigonia, and specialized leaflets act as envelopes or roofs and constitute the "perichætium". Sometimes these leaflets have the appearance of floral leaves, as, for instance, in the Hair-Mosses (*Polytrichum*), several species of which may be included amongst the commonest of our Mosses. The antheridia and amphigonia are here distributed on different individuals.

The investing leaflets at the summit of those stems which terminate in antheridia are crowded close together; they are short, broad, and of a brownish-red colour, and look like small floral-leaves seated upon a disc-shaped receptacle. *Polytrichum* is a typical instance of the Mosses which exhibit a conspicuous contrast between the investing scales of antheridia and those of amphigonia. The perichætium in individuals which produce only amphigonia possesses an altogether different form and arrangement of parts from the corresponding structure in antheridia-bearing individuals. They form a flask-shaped enclosure rather than a coloured flower-like structure, and later, from their midst arise stalked capsules in which the spores are borne. These capsules are the direct product of the amphigonia after they have been fertilized. The colouring of the antheridial involucres gave rise to the suggestion that insects might be concerned in fertilization. But there does not appear to be any evidence in support of such a view.

As before said, there is a close resemblance between Muscineæ and Characeæ as regards the position of the ooplasm to be fertilized in the middle of the amphigonium, the genesis and form of the spermatozoids, and, lastly, the process of fertilization. But from the moment of fertilization the course of development is altogether different. The fruits of Characeæ become detached from the mother-plant, whereas those of Muscineæ remain in connection with it, and this connection is not merely mechanical but organic. The generation developed from the Moss-fruit continues to derive the nutritive substances requisite for its growth and completion from the mother-plant, and without the support of the latter it would inevitably perish. The word support may here be used in a wide sense; for the mother-plant is actually the bearer or stay of the new generation, which is produced from the ooplasm converted by fertilization into an embryo, and it may be compared to a tree with Mistletoe growing upon its boughs. In Characeæ the separate stages of development are always quite distinct; the stage of maturity in particular being characterized by the falling away of the fruit from the mother-plant. This is not the case in Muscineæ. Since no separation in space takes place, it is also difficult to establish time-limits and to say when the fruit has attained maturity, and the difficulty is increased by the fact that no sufficient indications are afforded by alterations of shape or colour. It is best to look upon the formation of fruit as being complete as soon as fertilization has taken place; from this moment the ooplasm must be considered to be an embryo, and its envelopes to be fruit-coats. Evidence in favour of this conception of the phenomenon is afforded by the circumstance that after the union of ooplasm and spermatoplasm development is arrested, and a period of repose ensues, whereas both before and afterwards the outward manifestations of change follow one another in rapid succession. A description of the subsequent changes has been already given (see pp. 15, 16), and we need only repeat here that the generation which springs from the Moss-fruit develops spores and, after having scattered them abroad, dies away.

The strongest likeness exists between the fruit-rudiments and antheridia of Muscineæ and those exhibited by Ferns, Horse-tails, Rhizocarps, and Club-Mosses,

all of which are classed together under the name of Vascular Cryptogams, on account of the presence of vascular bundles in their stem-structures and phylloclades. The first generation of these Vascular Cryptogams, whereon are developed the antheridia and fruit-rudiments, also resembles in an unmistakable manner the first generation in certain Liverworts.

In Ferns, which constitute the most extensive section of the Vascular Cryptogams, and may be taken as their type, the first generation makes its appearance in the form of a flat, green, foliaceous structure, usually reniform or heart-shaped, lying in close contact with the nutrient soil (see fig. 189[16]). Inasmuch as the tissue of this first generation nowhere contains vascular bundles, it must be looked upon as a thallus, and has received the name of *prothallium*. The Fern-prothallium bears the fruit-rudiments as well as the antheridia upon its under surface, which is in contact with the nutrient soil, and which adheres to it by means of a number of delicate hair-like suction-cells. Some Ferns develop the fruit-rudiments and antheridia on separate prothallia; others produce them both on the same prothallium. In the latter case the fruit-rudiments are situated near the sinus of the prothallium, and the antheridia on the part remote from the sinus. Each fruit-rudiment may be compared to a flask in shape, and arises from a superficial cell of the prothallium which is only slightly arched outwards. This cell is divided by the insertion of two partition-walls into three cells, each of which is again segmented in definite directions. From the uppermost cell is produced a tissue which forms the neck of the flask-shaped fruit-rudiment; the middle cell gives rise to three cells, of which the two upper, the canal-cells, occupy the neck, whilst the undermost one becomes the relatively large and subsequently rounded ooplast. The daughter-cells developed from the lowest primary cell take the form of an investing wall round the ooplast, or, to return to the analogy of a flask, constitute the wall of the ventrally enlarged portion of the flask. The protoplasm of the ooplast is the ooplasm, and is now to be seen surrounded by a pluricellular tissue, which, as in the case of Characeæ and Muscineæ, may be called an amphigonium. Only the neck of the amphigonium projects above the other adjacent tissues of the prothallium; the enlarged ventral portion is, as it were, sunk in the substance of the prothallium.

The antheridia are also developed from cells upon the surface of the prothallium. These cells project in the form of papillæ above the surrounding tissue and undergo division by the introduction of partition-walls. The outermost daughter-cell becomes enlarged and assumes a globular shape, and from the protoplasm in its interior are formed spiral spermatozoids. Another mode of origin consists in the formation of a papilliform or hemispherical protuberance of tissue which shows unmistakably a differentiation into central cells destitute of chlorophyll and enveloping cells containing chlorophyll. The former divide up and a filling-in tissue is formed, the small constituent cells of which contain spermatoplasm. After the development of a spermatozoid in each of these small cells, the whole of the filling-in tissue falls to pieces, that is to say, the individual cells separate from one another and remain for a short time disconnected but still in

contact. At length the top of the antheridium opens; the loose cells are discharged into the surrounding water derived from rain or dew, and from each of them is set free a spirally-coiled spermatozoid furnished as regards its anterior half with bristling cilia (see vol. i. p. 29, fig. 7 [11]). The spermatozoids manifestly direct their course to an amphigonium as they whirl about in the water. Meanwhile the neck canal-cells of the amphigonium have been partially converted into mucilage; some mucilage is discharged into the environing water, and it seems that concomitantly with this organic acids have been evolved in the region of the amphigonium, which exercise an attractive influence on the spermatozoids. What is known as a fact is that the spermatozoids accumulate in this mucilaginous mass and also penetrate through the slimy substance left behind in the canal of the amphigonial neck. Thus they reach the ooplasm which is hidden in the oogonium at the bottom of the fruit-rudiment. As it has repeatedly been observed that spermatozoids make their way into the ooplasm and there disappear, we may assume that the delicate envelope of the ooplast is pierced by the spermatozoid, and that thereupon a coalescence between the two kinds of protoplasm takes place (*cf.* also figs. 346 [1, 2, 3, 4]).

The fertilized ooplasm now subdivides into several cells with partition-walls inserted between them, and thus is produced a multicellular embryo which remains embedded in the unaltered amphigonium. This structure, though scarcely differing at all from the fruit-rudiment, must be considered as a fruit. After a short period of rest the embryo germinates, and the new generation, which gradually makes its appearance as stem, roots, and fronds emerging from the embryo, continues for a short time to receive its food-stuffs through the mediation of the parental prothallium. At length, when the new generation has grown sufficiently strong, and is capable of taking up food-stuffs directly from the surrounding air and soil, and of transforming them into constructive materials, the assistance of the prothallium becomes superfluous. The prothallium then withers, and by the time the sporogenous fronds have developed it has vanished, and no trace of it remains.

The Horse-tails (Equisetaceæ) have, in the main, the same features as the Ferns just described as typical of the Vascular Cryptogams in all that relates to the forms of prothallium, antheridia, and fruit-rudiments. The prothallium produced from the spore is at first delicate and ribbon-shaped, but later becomes multifariously lobed, and in form recalls the thallus of certain Liverworts, or sometimes even resembles a little curled foliage-leaf. In most species antheridia and fruit-rudiments grow on different prothallia. Where this is not the case, fertilization of the ooplasm by spermatoplasm arising from the same individual is rendered impossible by means of a disparity between the organs concerned in respect of the time at which they mature. The prothallia which give rise to antheridia are always much smaller than those which produce the fruit-rudiments. The antheridia develop from superficial cells at the end or on the margin of the lobate prothallium, whilst the fruit-rudiments, on the other hand, are derived from superficial cells in the recesses between the lobes (see fig. 190 [8]). The spermatozoids

have a spatulate enlargement at one extremity, and carry on the other, attenuated end a regular mane of extremely fine cilia.

Far more important are the characteristics which distinguish from Ferns the Rhizocarpeæ and Lycopodiales, especially the genera *Salvinia*, *Marsilia*, and *Selaginella*, in all of which the development has been studied with great care. The antheridia-bearing prothallia are, in the last-mentioned genera, extremely different in point of size from those which bear fruit-rudiments. Both prothallia, it is true, have spores for their starting-points, but these spores themselves have different dimensions, and are distinguished as *microspores* and *macrospores* (*i.e.* small spores and large spores). The microspores are the parts of the plant where antheridia are formed, and the macrospores those where fruit-rudiments are formed. In a microspore the protoplasm divides into several parts, and partition-walls are inserted between them, thus forming a tissue composed of a very few cells, the greater part of which remains concealed in the interior of the spore. Only one or two superficial cells of this tissue push out through rents made here and there in the coat of the spore, and these protruded cells constitute the antheridia. The apical cell of the antheridium becomes filled with a tissue, and in each cell of this tissue is formed a spirally-coiled spermatozoid. The opening of the antheridium and the escape of the spermatozoids then ensues in the same manner as in Ferns. The prothallium which originates from a macrospore and is the seat of formation of fruit-rudiments, although it is larger and composed of more cells than that just described, does not forsake the interior of the cavity of the macrospore to any greater extent, but only protrudes a little at one place where the tough outer coat of the macrospore is ruptured. Two kinds of tissue are in reality developed within the limits of each macrospore, viz.: the one above referred to as emerging between the torn edges of the outer spore-coat, and a tissue of reserve material deposited at the bottom of the macrospore. The latter is very rich in starch and oil, and serves as a storehouse of nutriment for the prothallium at least until it is in a position to get food for itself out of the environment. The fruit-rudiments (amphigonia) appear on the protruding portion of the prothallium, and are entirely buried in its tissue. The development of the fruit-rudiment, the formation of canal-cells which subsequently turn into mucilage, the penetration of the spermatozoids, and the act of fertilization, are in all essential respects the same as the corresponding processes in Ferns, and therefore a description of them in detail may here be dispensed with.

The tissue produced from a macrospore in the Rhizocarpeæ and Selaginelleæ has been compared to the ovule as it occurs in the Phanerogams which will be the subject of the next chapter, and certain actual analogies have been brought out which are exhibited by the ooplasm when converted into an embryo, the store-chamber for food-stuffs, and the protective envelope in each case. Having regard to the identity of object aimed at through the instrumentality of these structures in the most widely different sections of the Vegetable Kingdom, such analogies are really a matter of course, and if naturalists limit themselves to proving that organs

which have the same functions, however greatly they may differ in form, yet always possess certain similarity, and that this similarity increases in a conspicuous degree when the external conditions of life are the same, no objection can be made to the generalization. But if it is made the basis of far-reaching speculations and of hypotheses concerning the evolution of one group of plants from another, the descent of Phanerogams from Cryptogams, for example, I must enter an emphatic protest against any such proceeding.

THE COMMENCEMENT OF THE PHANEROGAMIC FRUIT.

Long experience has shown us that the propagation of plants is accomplished with much greater certainty by means of Brood-bodies than by Fertilization and production of Fruit. For a fruit to be formed, two portions of protoplasm which have arisen separately must be brought together. Such a union denotes that at least one of the two protoplasts in question is endowed with a capacity for translation, that the male cell is not obstructed on its way to the female, and that facilities are present to promote its union with that cell. But there's many a slip 'twixt the cup and the lip! Adverse winds, unfavourable currents, long-continued drought, uninterrupted rain, these and many another unexpected circumstance may bar the way to fertilization. Often enough fertilization is hindered from causes such as these, and in consequence the young fruit-rudiment atrophies, the embryo is not formed, and the plant, in order to propagate, must rely on its brood-bodies.

That fruits do not miscarry oftener than they actually do is due to the fact that the difficulties of the situation from external cause, are to some extent met by the position of the egg-cell and the form of the young fruit. In other words, the fashioning of the organs concerned in the production of fruit is adapted to the circumstances of the environment.

Perhaps the obstacles are at a minimum in the case of plants in which fertilization is accomplished under water. The cells in question here require no especial protection. The surrounding water maintains them in the proper position, brings food to them, and protects them from drying up. In it they both live and move. Thus it is intelligible why so many plants which live under water, or which use water for the accomplishing of fertilization, are destitute of any but the simplest envelopes for their spermatoplasm and ooplasm. Complicated investments are valueless under such circumstances, possibly even disadvantageous; in any case they are superfluous. Nor is it usual in plants to produce superfluous structures. As we know, aquatic plants do not possess woody stems and branches. And for this reason. Tissues of this kind are not required, since the surrounding water buoys them up in the proper position so that hard wood and bast are not needed. So also with the ooplasm and spermatoplasm. Cryptogamic plants which fruit under water do not possess complex ovaries like Phanerogams, as they are unnecessary. Just before the time of fertilization the

spermatoplasm is segmented up into many fragments; these escape from the antheridium and reach the simple fruit-rudiment by swimming. Since the spermatozoids are attracted to the young fruits by certain excretions which the latter pass out into the water, the multifarious devices associated with aërial fertilization are unnecessary. Protective coats around the sexual organs, sheaths to limit evaporation, brightly-coloured or sweet-smelling floral-leaves to attract insects that they may transfer the pollen from flower to flower—all these are wanting in plants which are fertilized under water. Now it is just these accessory protecting structures which constitute what are called blossoms. Thus we can say that these water-plants have no blossoms. To avoid misconception it must be stated that although they have no blossoms they have flowers. For although, popularly, blossoms and flowers are used as synonymous terms, under flowers are comprehended the organs which are concerned in fertilization, under blossom merely the leaves which inclose the essential organs and which guard and protect the young fruits and stamens. It is these latter which produce the sexual protoplasts. Their union is promoted by the leaves of the blossom. Sometimes they catch the pollen-grains as they are blown by the wind, or by the production of honey and scents attract insects which remove the pollen in their visits. In other cases, by projecting ridges and corners, they are instrumental in detaching the pollen from these same insects, and in a thousand ways protect and assist the difficult process of aërial fertilization.

In the above lines we have been speaking not of aquatic plants generally, but of such as are fertilized under water. And these should be carefully distinguished. Many aquatics, which pass their lives under water, send up their flowers to the surface so that their fertilization is aërial. On the other hand, strange though it may seem, the fertilization of most aërial Lichens, Mosses, and Ferns which grow on the sand of desolate moors, on the sunny rocks of mountain sides, or on the dry bark of old tree stems, is accomplished under water. Plants of this sort may be exposed to drought for many months, and the movement of sap within them may be suspended; but when they are moistened with rain or dew they are quickened and rejuvenated, and form their young fruits and antheridia. Things are so arranged that the liberation of the spermatozoids coincides with the moment at which these plants have access to sufficient moisture. Thus we see that it is literally true of these plants—whether growing on the bough of a tree or in a ravine on a mountain side—that their fertilization is accomplished under water.

The only really important distinction between plants permanently submerged and such as are thus situated from time to time, is that in the latter the young sexual organs are protected against desiccation during the periods of exposure by means of sheathing structures and leaf-like scales, as is particularly well shown by the Mosses. Blossoms in the usual sense, however, are not found amongst Ferns and Mosses, and we can make the following three general statements:—(1) That Cryptogams are fertilized under water and most Phanerogams in the air; (2) that

Cryptogams lack blossoms, since these are not necessary for aquatic fertilization; (3) that almost all Phanerogams, on the other hand, possess blossoms, since they are required to protect and promote aërial fertilization.

The very complicated structure of the parts immediately adjacent to the region where the sexual protoplasts are developed depends upon the fact that fertilization is aërial. The portions of protoplasm destined for fertilization can only be adequately elaborated if their enveloping membranes are thin and delicate, and suited for the osmotic transfer of materials. Such a membrane, however, is incapable of protecting the protoplasm from the drying influence of the air; it is absolutely essential that both the spermatoplasm and the ooplasm shall be protected during the critical period by a suitable envelope. Thus one finds in all Phanerogams—quite apart from the perianth—a protective mantle developed around the sexual cells. This mantle has its cell-walls suitably thickened; its outer layers afford the necessary resistance to desiccation, whilst deeper down an ample supply of water is maintained.

These characters are well shown in that constituent of the ovary from which the seed will be ultimately produced. This portion is known as the *ovule*. Every ovule consists of a mass of tissue, the *nucellus* of the ovule in which the ooplasm or egg-cell is concealed, and an enveloping sheath, the *integument*, which may be either single or double. Such ovules are borne in the genus *Cycas* (figs. 208[7] and 208[8]) without further covering than a fretwork of hairs which protects them against too great drying up. In other Cycads and in the majority of Gymnosperms, of which the Cypress and Juniper, the Pine and the Fir, may be quoted as examples, the leaf-like scales of the young fruit are so arranged that the ovules produced on their surfaces are hidden from view and secure against outside danger. In the other Phanerogams (the Angiosperms) the ovules are concealed in a closed chamber—the pistil—the lower enlarged portion of which is known as the *ovary*.

In the construction of this chamber the chief part is taken by the floral axis and by the floral-leaves known as *carpels*. So unequal, however, is the share taken by these parts in the structure of the ovary that in some cases it is formed almost entirely from the floral axis, and in others almost entirely from the carpels. In consequence the apex of the floral axis, which is known as the floral *receptacle*, shows an extraordinary variety of form. Thus in one series of plants the receptacle is not excavated, but solid, assuming the form of a knob, hemisphere, or cone (figs. 207[8] and 207[9]); whilst in others it is concave and excavated (figs. 208[1] and 208[2]). The forms met with in nature can be produced artificially by taking a conical mass of soft wax and flattening its summit, then gradually pressing it down into a saucer-like shape, and so on until one has produced a hollow bowl. So in nature we have at one extreme the solid cone, at the other the hollow vessel. Between these two extremes, between the conical and excavated receptacles, we have the flat or disc-like receptacle. It is hardly necessary to point out that in the growth and differ-

entiation of the living plant the excavated receptacle is not the result of any actual hollowing-out process as in the lump of wax, but is due to unequal growth of the different parts of the receptacle—the peripheral parts growing up as a circular wall around the central parts, so that the form of a cup or urn is gradually assumed. When one speaks of the excavation of the receptacle one is speaking figuratively—there is no excavation in a literal sense.

The configuration of the receptacle is further complicated by the fact that

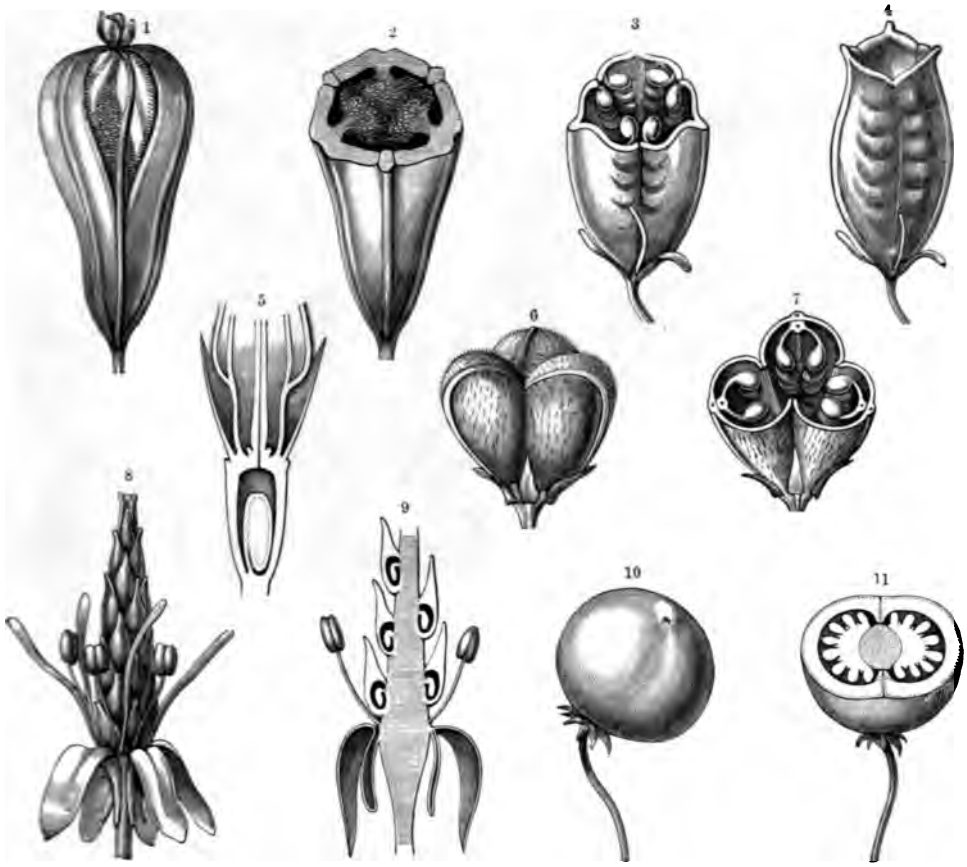

Fig. 207.—Structure of Phanerogamic Ovaries.

[1] Dehisced fruit of *Miltonia stellata*. [2] Ovary of *Miltonia* cut across transversely. [3] Ovary of Mignonette (*Reseda*) cut across transversely. [4] The same ovary intact. [5] Longitudinal section of the ovary of the Jerusalem Artichoke (*Helianthus tuberosus*). [6] Ovary of the Violet (*Viola odorata*). [7] The same, cut across. [8] Receptacle and carpels of *Myosurus minimus*. [9] The same in longitudinal section. [10] Young fruit of Potato (*Solanum tuberosum*). [11] The same cut transversely. All the figures considerably magnified.

the centre of the receptacle does not always cease growing, but grows up as a cushion or peg; thus we have a receptacle having the form of a conical peg with a peripheral, urn-like wall around it.

In describing the relations of the floral-leaves to the receptacle it will be simplest to commence with the conical receptacle. Here the floral-leaves are found arranged in whorls above one another or in a continuous spiral. At the top are the carpels, below these the stamens, and below these again the leaves

of the perianth. Of these various kinds of leaves there may be developed one, two, or even more whorls. When several whorled carpels are united together so as to inclose a single chamber, the tip of the receptacle may be produced above the point of insertion of the carpels and project into the ovarian cavity, or it may penetrate the ovary as a central column. On the other hand, each carpel may give rise to a separate chamber, in which case one finds a whorl of distinct

Fig. 208.—Structure of Phanerogamic Ovaries.

[1] Excavated receptacle and carpels of a Rose (*Rosa Schottiana*). [2] The same in longitudinal section. [3] A single carpel of the same in longitudinal section. [4] Ovary of the Apple (*Pyrus Malus*) in longitudinal section. [5] The same in transverse section. [6] Transverse section of a ripe Apple. [7] Carpel of *Cycas revoluta* with ovules. [8] Longitudinal section of an ovule of *Cycas*. [1, 6, 7, 8] natural size; [2, 4, 5] ×3; [3] ×8.

ovaries at the tip of the receptacle (fig. 210[7]); or there may be numerous small ovaries spirally arranged around the receptacle (figs. 207[8] and 207[9]).

In order that the position and mutual relations of the various floral-leaves on disc-like and excavated receptacles may be intelligible it is necessary that we should return to the lump of wax. Let the cone of wax be pressed down so that it assumes the form of a disc or cup. Assuming the floral-leaves to be present upon it during this process—covering the cone from base to apex—when the disc stage is reached the leaves formerly present at the apex will occupy the centre, those at the base the periphery of the disc. If the wax be further moulded into a cup the leaves previously at or near the apex of the cone will

occupy positions within the cup—those immediately at the apex being at the centre—whilst those near the base will be found on the edge of the cup.

According as the leaves are inserted spirally or in whorls upon the receptacle, whether they are present in single or double cycles, whether they are fused with one another or with the receptacle—all these offer almost infinite possibility of variation in form, so manifold, indeed, that their complete description is quite beyond the limits of the present work. Here the forms described must be limited to a series of more or less typical cases; they are for the most part selected from well-known and widely-distributed plants readily accessible to any one.

To avoid repetition the seventeen selected cases are arranged in two groups, of which the first group includes forms with a conical receptacle, the second such as have a disc-like or excavated receptacle. Each of these groups is further subdivided, according as the carpels are all of one sort or of two sorts.

OVARIES ON A CONICAL RECEPTACLE.

Carpels all of One Sort.

(1) The carpels are inserted spirally on the receptacle. Each carpel contains one or several ovules. The receptacle is either much elongated, as in the Mousetail (*Myosurus*, figs. 207[8] and 207[9]), or conical, as in the Tulip-tree (*Liriodendron*), or button-like, as in the Crowfoot (*Ranunculus*).

(2) The carpels are inserted in whorls upon the receptacle, their margins are infolded and fused with the prolonged apex of the receptacle. Since they are also fused with one another below, they collectively form a multilocular ovary. Each carpel bears ovules over its inner surface. As examples may be quoted the Yellow Water-Lily (*Nuphar*), and the Flowering Rush (*Butomus*, figs. 210[7] and 210[8]).

(3) The carpels are inserted in a whorl at the summit of the receptacle and are fused with one another. The receptacle does not project into the ovarian cavity. Each carpel bears ovules either along its margins, as in Mignonette (*Reseda*, figs. 207[3] and 207[4]), or on its internal surface, as in the Sundew (*Drosera*), or basally, as in *Dionæa*, *Drosophyllum*, and in *Caylusea* (Resedaceæ). In *Reseda* the ovary is open above.

Carpels of Two Kinds.

(4) The carpels arise at the tip of the receptacle in two alternating whorls of two each. The two upper carpels are reduced to midribs on which the ovules are borne in two rows. A delicate membrane is stretched like a tympanum between these two midribs which form the frame. The two lower carpels are destitute of ovules and are fixed like valves to the upper pair. This form is met with in numerous modifications in the Cruciferæ.

(5) The carpels arise in two whorls at the tip of the receptacle. Those of the lower whorl are destitute of ovules and form the ovary, those of the upper whorl are modified into strings or cushions, and are fused with the inner surface of the

lower carpels. They bear the ovules. Examples:—the Violet (*Viola*, figs. 207 [6] and 207 [7]), the Celandine (*Chelidonium*), and the Poppy (*Papaver*).

(6) The lower whorl of carpels are united edge to edge, inclosing the ovarian cavity. They are destitute of ovules. The tip of the receptacle projects a very short distance into the ovary, and bears a single ovule-bearing carpel which is apparently terminal upon it. Examples:—the Rhubarb (*Rheum*), and Dock (*Rumex*, fig. 212 [23]).

(7) The lower whorl of carpels are united edge to edge like staves, forming the ovary into which the apex of the receptacle projects as a central column. The upper ovuliferous carpels are metamorphosed into cushion-like structures consolidated with the receptacular column. These cushions are either arranged spirally, as in *Glaux* (figs. 211 [8] and 211 [9]), or in a whorl, as in *Primula Japonica*.

(8) The lower carpels are inserted in a whorl, and have their margins infolded, and are fused together so as to form a multilocular ovary. The upper, ovuliferous carpels arise from the tip of the receptacle, which is continued through the centre of the ovary. The ovules project into the cavities of the ovary. Examples:—The Spurge (*Euphorbia*), *Azalea*, Foxglove (*Digitalis*), Potato (*Solanum*, figs. 207 [10] and 207 [11]).

OVARIES ON A FLAT OR EXCAVATED RECEPTACLE.

Carpels of One Sort.

(9) The carpels are arranged spirally upon a raised central cushion of the *flat* receptacle. Each carpel forms a distinct ovary containing one or more ovules. Examples:—*Dryas*, *Potentilla*, the Raspberry (*Rubus Idæus*, figs. 210 [11] and 210 [12]).

(10) The carpels are arranged spirally within an *excavated* receptacle. Each carpel forms a distinct ovary containing one or more ovules. There is no fusion between the walls of the carpels and that of the receptacle. Example:—The Rose (*Rosa*, figs. 208 [1, 2, 3]).

(11) A single ovuliferous carpel is inserted in the centre of an excavated receptacle. It is apparently terminal upon the axis, and is not fused with the excavated receptacle. This condition prevails in the Cherry, Plum, Apricot, and Almond (*Amygdalus*, figs. 209 [6] and 209 [7]).

(12) The carpels arise in a whorl from the end of the axis at the base of an excavated receptacle. Their margins are infolded, and they are fused together into a multilocular ovary. The ovary fills the whole cavity of the receptacle, with the inner wall of which it is fused. Ovules are borne by the infolded margins of each carpel. Examples:—The Medlar (*Mespilus*), Pears and Apples (*Pyrus*, figs. 208 [4, 5, 6]).

(13) The carpels arise from the tip of the axis at the base of the excavated receptacle. The receptacle has a remarkable structure; it is like a bottle in shape with three portions of the wall removed, so that it is reduced to three ribs which join above and bear the other parts of the flower. The apertures in the receptacle are occupied by the three carpels. Thus the ovary consists of three carpels and

three receptacular ridges. The ovules are borne on longitudinally-running cushions on the carpels. This class of ovary is found in great variety amongst the Orchidaceæ (figs. 207 [1] and 207 [2], and figs. 212 [1, 2, 3, 4]).

Carpels of Two Kinds.

(14) One series of carpels, destitute of ovules, arise from the margin of the deeply-excavated receptacle, roofing it in. Another series, metamorphosed into

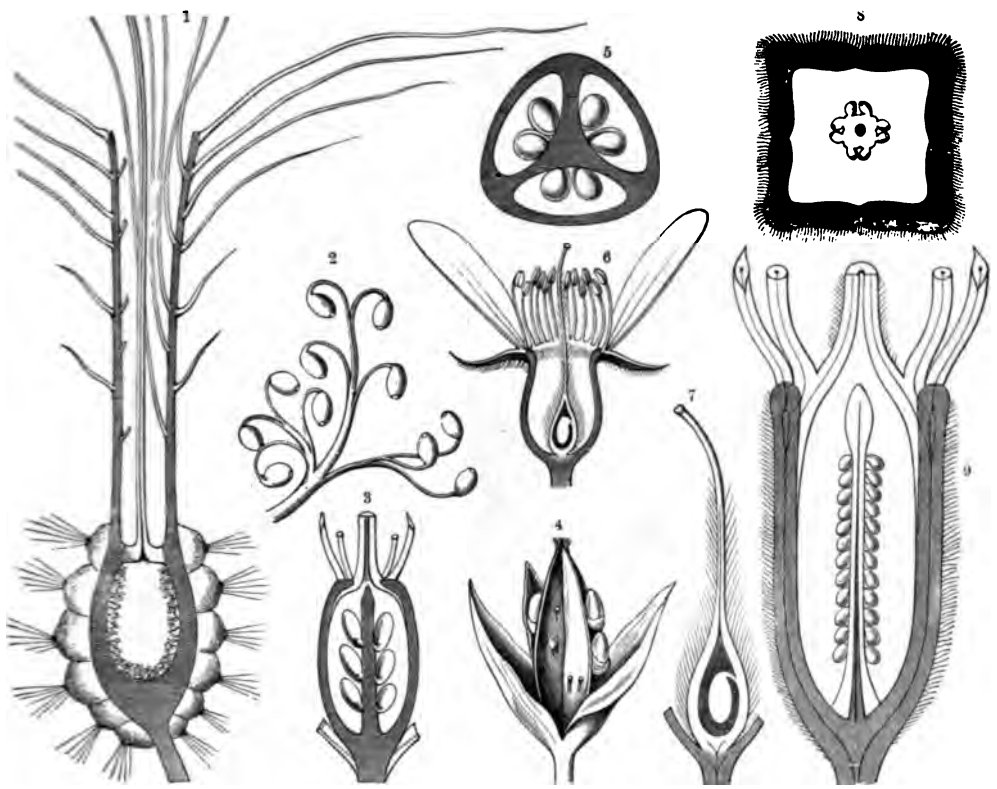

Fig. 209.—Structure of Phanerogamic Ovaries.

[1] Longitudinal section of the ovary of *Cereus grandiflorus*. [2] Ovules on a branched placenta from the base of the ovary of *Cereus*. [3] Longitudinal section of the ovary of *Hedychium angustifolium*. [4] Dehisced fruit of the same plant. [5] Transverse section of the ovary of the same. [6] Longitudinal section of an Almond flower (*Amygdalus communis*). [7] Longitudinal section of the ovary of the same. [8, 9] Transverse and longitudinal sections of the ovary of the Willow-herb (*Epilobium angustifolium*). [1] natural size; [2, 4, 5, 6] slightly magnified; [3, 7, 8, 9] ×10.

ovule-bearing strings, arise spirally from the inner wall of the receptacle and project into the ovarian cavity. Examples are afforded by the Cactaceæ, *e.g.* *Opuntia* and *Cereus* (figs. 209 [1] and 209 [2]).

(15) One series of carpels closes the mouth of the excavated receptacle, as in (14). The other series, bearing the ovules, are filamentous, and arise as a whorl from the base of the receptacle; they are consolidated with a thread-like prolongation of the tip of the axis which runs up as a central column. Example:—The Willow-herb (*Epilobium*, figs. 209 [8] and 209 [9]).

[These two figures are slightly inaccurate in that the partitions of the ovarian cavity are not indicated. In the cross-section, fig. 209 [8], they would run diagonally from the corners to the central column. In allied forms they are sometimes incomplete.—*Ed.*]

(16) One series of carpels as in (14) and (15). The other series are metamorphosed into ovuliferous cushions spirally inserted on a continuation of the axis

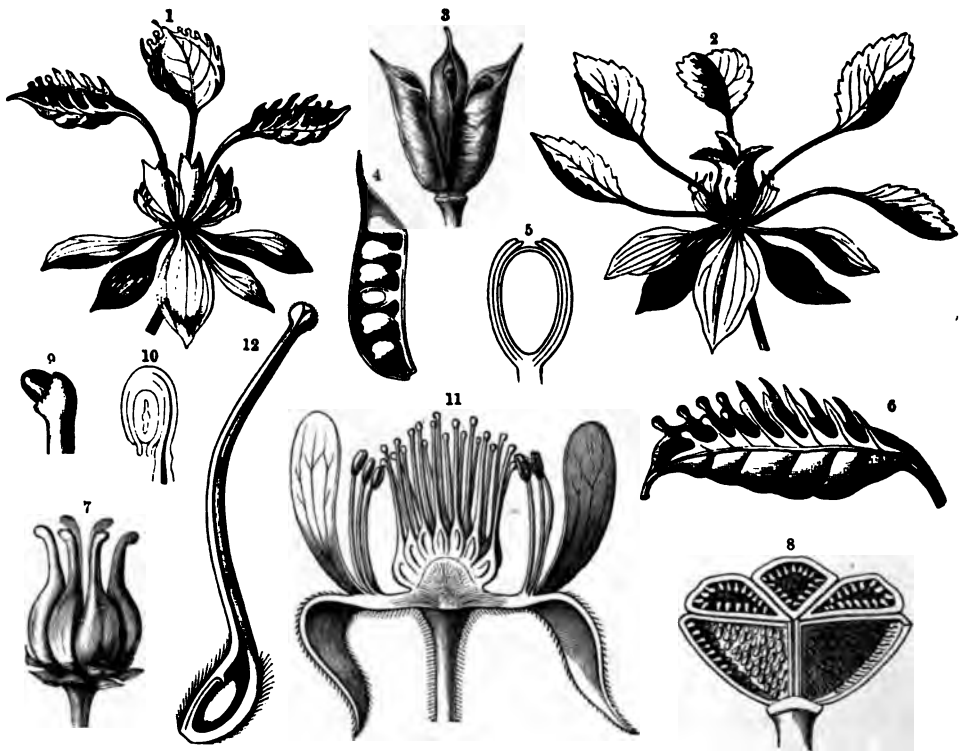

Fig. 210.—Structure of Phanerogamic Ovaries.

1, 2 Antholysis or Chloranthy of a Larkspur (*Delphinium cashmirianum*). 3 Ripe dehiscing fruit of same. 4 Longitudinal section of a single carpel of same. 5 Longitudinal section of an ovule of the same. 6 A single foliaceous carpel of same. 7 Pistil of *Butomus umbellatus*. 8 Pistil of same dissected. 9 Young ovule of same. 10 Full-grown ovule of same in longitudinal section. 11 Vertical section of flower of Raspberry (*Rubus Idæus*). 12 Longitudinal section of a single carpel of the same. 1, 2, 3 natural size; 4, 6, 7, 11 magnified 2-5 times; 5, 8, 9, 10, 12 magnified 6-8 times.

which rises up from the base of the receptacle. Example:—*Hedychium* (figs. 209 [3, 4, 5]).

(17) As before, one series closes the mouth of the receptacle. From the tip of the axis at the base of the receptacle a single apparently terminal carpel arises which bears a single ovule. This condition obtains with many variations in the Compositæ, *e.g.* the Sunflower (*Helianthus*, fig. 207 [5]).

The account of the structure of the ovary just given differs in several fundamental points from the current views of the best authorities in plant morphology. Especially is this so in two points. Firstly, in that the wall of

so-called "inferior ovaries" consists, for the most part, according to my own investigations, of a deeply excavated receptacle and not of carpels invested by the tube of the calyx or perianth. That the latter condition occurs (as in many

Fig. 211.—Antholysis and Structure of the Ovary.

1–5 Longitudinal sections of the ovaries of "monstrous" flowers of *Primula japonica*; the outer carpels form the ovarian cavity and are destitute of ovules; the inner carpels show all transitions between ovuliferous cushions, concrescent with the extremity of the axis, and isolated leaf-structures, the marginal teeth of which correspond to ovules. 7 A single "monstrous" flower of *Primula japonica*. 8 Longitudinal section through the ovary of *Glaux maritima*. 9 View into the ovary of same after removal of the front wall. 7 natural size; the others magnified 6–8 times.

Saxifrages) is not here denied, but more frequently is it the receptacle which is raised as a circular wall to form a closed ovary. On the ripening of the fruit the capsule in many cases opens by means of valves which strikingly resemble the valves formed from true carpels. It is, however, but a resemblance comparable to that existing between the phylloclades of Butcher's-broom and true leaves (*cf.* vol. i. p. 333).

A second divergence from recognized views is the assumption that two kinds of carpels take part in the formation of many ovaries, *i.e.* an outer series, destitute of ovules, forming the ovarian cavity, and an inner, ovuliferous series variously metamorphosed into cushions, strings, ridges, &c. This view is supported not only by extensive investigations into the development of ovaries, but also by a number of cases of antholysis which throw considerable light on obscure points of ovarian morphology.

As we shall refer frequently to this state of *Antholysis* it will be well to state at once, briefly, exactly what is meant by the term. Everyone is acquainted with the "double flowers" of Roses, Snowdrops, Carnations, Primroses, Tulips, &c., so common in cultivation. Into the cause of their origin we shall inquire later on; here it is sufficient to note that in double flowers we find (1) that the stamens are entirely or in part transformed into petals, occasionally into carpels; (2) that a multiplication of the perianth-leaves, stamens, and carpels is apparent, and (3) that with this change is often combined a *greening* of the parts not usually green, and (4) a general loosening and separation of parts which in ordinary, single flowers are fused with one another. Especially do we find those leaf-structures which normally are united to form the ovary loosened and increased; they are produced as flattened structures, having much the appearance of green leaves. One finds frequently all possible transitions in one and the same flower, so that the various stages in the conversion of carpels into green leaves can be readily followed.

In cases of antholysis where the parts of the ovary show a transformation into green leaves, one feels justified in regarding the structures in question as foliar in nature. Especially is this so when none of the ascertained facts of development militate against this view. In the same way such parts as never assume the forms of leaves in these "loosened" or segregated flowers may be interpreted as stem-structures—always provided that developmental history harmonizes with this view.

In the cursory review of types of ovarian structure given in the last few pages it was stated that in some cases carpels of one kind only are present, whilst in other cases carpels of two kinds contribute to the formation of the ovary. This statement is based in part on facts gleaned from an examination of these loosened, antholytic, or so-called "monstrous" flowers. The antholytic flowers of a Larkspur (*Delphinium cashmirianum*) reproduced in figs. 210 [1-6] show unmistakably that only a single whorl of carpels is present and that each of them bears ovules on its margins. Similarly those of the Japanese Primrose (*Primula japonica*) represented in figs. 211 [1, 2, 3, 4, 5, 6, 7] demonstrate that here two sorts of carpels are concerned, *i.e.* outer foliaceous ones destitute of ovules, and inner ovuliferous ones modified into a cushion.

Having described the chief forms assumed by the ovarian cavity, we may pass on to speak of its most important contents, the *ovules*. All ovules agree in this: that at the time of fertilization they consist of masses of tissue, exhibiting a differentiation into central and peripheral cells, and also in the fact that one of the cells of the central portion is destined to become an embryo. In the majority of

flowering plants we find a definite central mass of cells, the *nucellus*, surrounded by a well-marked sheath, the coat or *integument*. Generally the integument is double, as in *Delphinium* and *Butomus* (*cf.* figs. 210[5, 9, 10]), in other cases it is single, as in Compositæ, Umbelliferæ, *Hippuris* and *Cycas revoluta* (*cf.* fig. 208[8]). In most Orchids the nucellus is inclosed in a large-celled, inflated and transparent integument, through which it is distinctly visible (*cf.* fig. 212[5]). In not a few epiphytic Orchids, however, this contrast of parts is only imperfectly shown, whilst in the Balanophoreæ and various other parasites no trace of the distinction into nucellus and integument is found. In all cases where an integument is present it is discontinuous at one point, where the nucellus is uncovered. This is the *micropyle*. Sometimes the micropyle is at the apex of the ovule, but in a very large number of cases the whole ovule is bent over so that the micropyle is situated close to the point of attachment of the ovule. The ovule may be attached to its support (*placenta*) by means of a filamentous cord, or it may be directly seated upon it. The common condition of an inverted ovule fused with its filamentous stalk is shown in figs. 208[8] and 210[10]. The filamentous stalk is technically known as the *funicle*, and the ridge where it is fused with the ovule as the *raphe* (*cf.* vol i. p. 644).

The cells of the nucellus of the ovule show a very unequal growth. One of them enlarges in a conspicuous manner, and is known as the *Embryo-sac*. In Conifers it attains relatively to the other cells of the nucellus enormous dimensions, whilst in most other flowering plants as it grows it encroaches upon the other cells of the nucellus till only a single layer remains surrounding it. And even this layer may be in part absorbed, so that the embryo-sac actually penetrates to the micropyle. The protoplasmic contents of the embryo-sac is richly vacuolated, but at the end directed towards the micropyle vacuoles are absent, and the protoplasm breaks up into several distinct protoplasts, each of which is provided with a conspicuous nucleus but in the first instance with no cell-membrane. As a rule three such protoplasts are found at the micropylar end of the embryo-sac; of these one only gives rise, after fertilization, to an embryo. This cell is the *ooplast* or "germinal vesicle", the other two are named *synergidæ* (*cf.* also, figs. 315 and 316).

In the ovaries of Orchids, as shown in figs. 212[1, 2, 3, 4], the ovules arise in great numbers upon peculiar furrowed ridges of the carpels. They arise from the superficial cells of these ridges, and are not provided with any vascular-bundle connections; in fact, they are comparable to those epidermal structures known as hairs or trichomes. This analogy is emphasized by the fact that in the ovaries of many Orchids real hairs are present, as, for instance, in *Lælia Perrinii* and *Cœlogyne plantaginea*, transverse sections of which are represented in figs. 212[1, 2, 3, 4]. In these remarkable species six ridges project from the wall into the ovarian cavity, and from all of these hair-like structures are developed. The three ridges belonging to the curious excavated receptacle, already described, alone bear ordinary unicellular hairs, the others bear ovules, one of which is shown in fig. 212[5].

The ovules of Cycads are very differently developed, as may be seen from a

reference to fig. 208[7]. Here no ovarian cavity is formed, the carpels are distinct from one another, and are spirally inserted upon the termination of the caudex; they are deeply lobed, certain of the segments being transformed into ovules.

Thus, while the ovules of Orchids seem to be equivalent to hairs, those of Cycads represent leaf-segments. In both cases the relations of the parts seem obvious. But in a great many cases the significance of the ovules is by no means so obvious, especially when the developmental history admits of various interpretations. In such doubtful cases antholysis offers a welcome assistance—that is, where this "loosening" and "greening" involves not only the ovary but also the ovules.

Especially valuable in this respect are certain cases of antholysis of the flowers of the Sundew (*Drosera*). Whilst in the normal flowers of this plant the ovules arise on the inner surface of the united carpels, in the foliaceous or antholytic ones they are borne upon the open and isolated carpels as glandular tentacles, like those usually occurring upon the leaves of this plant (*cf.* fig. 212[6]). On many of the carpels these glandular structures are fused together in little clusters (212[7]), and these fused structures show various transitional stages leading up to inverted ovules (figs. 212[8, 9, 10, 11, 12]). From a study of these cases one may infer that the integument of the ovule here is equivalent to a group of tentacles.

Very different is the case of the Larkspur (*Delphinium*). In normal flowers the ovules arise from the infolded margins of the carpels, each of which forms an ovary (*cf.* fig. 210[4]). But in the foliaceous flower the carpels are open and their margins lobed (*cf.* fig. 210[6] and fig. 212[13]). They recall the carpels of Cycas (fig. 208[7]) and agree with it in that some of the segments are converted into ovules. And it must be especially noted that the leaf-segments are so folded that a pit-like excavation is formed (*cf.* figs. 212[14] and 212[15]). Thus it appears that in the Larkspur the ovular integument is formed by the folding of the leaflet-like segments. Different again is the case of the Clover (*Trifolium*), of which an antholysis is shown in fig. 212[16]. The ellipsoidal ovules, which are borne along the fused margins of the infolded carpel in the normal flower, are here replaced by little, leafy structures resembling leaflets on the margin of the open carpel (*cf.* figs. 212[16] and 212[17]). These leafy structures are neither rolled up nor folded, and from each projects the nucellus of an ovule, or rather a mass of tissue corresponding to a nucellus, surrounded by an enveloping wall (*cf.* figs. 212[18, 19, 20, 21]). This wall may be regarded as representing the inner integument of the ovule, whilst the outer one is replaced by a leaflet. The monstrous ovules in the ovary of the Common Sallow (*Salix Caprea*, fig. 212[29]) show similar relations, except that the green, leafy structure upon which the nucellus of the ovule is inserted is folded along its midrib and has a fimbriated margin (fig. 212[30]). Of especial interest are the monstrous flowers of *Rumex scutatus* (*cf.* fig. 212[24, 25, 26, 27, 28]), a plant common on the débris slopes of limestone mountains. In the normal flower of this plant the ovary is egg-shaped, and consists of three carpels united edge to edge (figs. 212[22] and 212[23]). But in these monstrous cases it is enlarged from six to tenfold, and modified into a funnel-shaped tube open above (212[24, 25, 26, 27]). From this the ovule, also modified into a tube, sometimes

Fig. 212.—Ovules and Foliaceous Carpels.

[1] Transverse section of the ovary of *Lælia Perrinii*; natural size. [2] A portion of this section; ×6. [3] Transverse section of the ovary of *Cœlogyne plantaginea*. [4] A portion of this section; ×6. [5] A seed of *Cœlogyne plantaginea*. [6] Antholysis of the flower of Sundew (*Drosera intermedia*). (After Planchon.) [7–12] Isolated portions of this flower. [13–15] Isolated portions of a similar flower of *Delphinium elatum*. (After Cramer.) [16] Antholysis of *Trifolium repens*. [17–21] Isolated portions of the same. (After Caspary.) [22] Flower of *Rumex scutatus*. [23] The same flower in longitudinal section; magnified. [24–28] Isolated portions from an antholysis of *Rumex scutatus*. (Partly after Peyritsch.) [29] Longitudinal section through the pistil of a "monstrous" flower of *Salix caprea*. [30] Foliaceous ovule from this pistil. [6–30] slightly magnified.

projects (212 [24]), or it may remain concealed within (212 [27]). Inside the ovular tube arises a little protuberance which may be regarded as equivalent to the nucellus of

the ovule. It is sometimes attached to the wider end of the tube (212 [25]), but more frequently it arises from the narrowed base as a tiny, conical projection inclosed in a circular envelope of its own (212 [28]). This envelope corresponds to the inner, and the tube to the outer integument of the ovule.

From a study of these monstrous flowers it would appear that when the ovule possesses two integuments, the outer one corresponds sometimes to the whole apical portion of a carpel, sometimes to but a segment of a carpel; the former being the case when carpels of two kinds are present, and when, at the centre of the floral receptacle, above the outer non-ovule-bearing carpels, only a single fertile carpel is produced. The inner integument, on the other hand, arises like a corona from the leaf-like outer one.

The nucellus of the ovule arises in many instances (*e.g.* in Orchids) from a mass of tissue produced by the division of a single epidermal cell, but in by far the majority of cases at the margin or upon the surface of a leaf or leaf-segment, resembling in all respects a foliar bud.

That the ovule can be produced directly from the floral receptacle is not yet ascertained with certainty, though such an origin would appear to be not improbable in the Pepper family. That is no good reason why ovules should behave differently from bud-like brood-bodies, which arise sometimes from leaf- and sometimes from stem-structures. So great is the analogy between ovules and detachable buds, that ovules formerly received from Botanists the name of "seed-buds". In this connection it is very instructive to contrast the ovules in the ovary of certain Orchids with the foliar buds produced on the leaves of some of these plants. In *Malaxis paludosa* (*cf.* fig. 200 [5], p. 41) the foliar buds are found partly on the upper surface of the leaf, partly on the margins, forming in the latter case a fringe. They consist of a compact, central portion inclosed in a large-celled envelope which is so fashioned that the whole structure resembles an ovule (*cf.* fig. 200 [6]). So striking is this resemblance, that anyone unacquainted with the fact that these buds arise from foliage-leaves would unhesitatingly regard them as ovules. Later on, of course, differences appear, in that in the ovule an independent embryo is produced, whilst the bud gives rise to a shoot, which must be regarded as a branch of the parent plant. This is, of course, an important distinction, and applicable to the majority of cases, though not quite to all. The parthenogenetically produced brood-bodies, to be treated fully by and by, have both the form of true embryos and occupy the same position in the ovule beneath the micropyle. Were it not known that the hard, indehiscent fruit (achene) of *Gnaphalium alpinum* (= *Antennaria alpina*), with the rudiment of another generation which it contains, is produced without the intervention of pollen, without fertilization, it would certainly not be apparent from its structure. From this we may conclude that the distinction between bud and ovule, between brood-body and fruit, cannot be based on purely structural characters, and that fruits and brood-bodies are sometimes interchangeable—facts of great importance in solving the question of the importance of fertilization in the origin of new species.

STAMENS.

As the last patches of snow disappear from the fields, the Snowdrop raises its white bells, and the catkins of the Willow break through the bondage of their bud-scales; in the copses likewise, where the warm March sunbeams penetrate, the Hazel begins to blossom and sheds its powder. These are the signs that spring is coming, and that the long winter is over. For some time the flowers both of the Snowdrop and Hazel have been ready—in the Snowdrop under ground, wrapped up in sheathing leaves; in the Hazel on the twigs as short, cylindrical, dusky catkins. With the advent of spring the catkins stretch and their crowded flowers are separated, they becoming flexible and hang like golden tassels from the branches, swaying in the wind and giving off their clouds of dust.

To this powder, long known to be connected with the fruiting of plants, the name of flower-dust has been given. This term, suitable in so many cases, has been used in others for a substance which, although corresponding in function to the flower-dust of the Hazel, differs from it in appearance. The cells which take the form of dust in the Hazel assume in other plants the form of sticky, viscous lumps, of spindle-shaped masses or granulated bodies, to which the designation dust is quite inappropriate. Were the species of plants whose flowers do not produce dust but few the term could stand, but when we find belonging to this category many of the principal families of plants—ten thousand Composites, eight thousand Orchids, five thousand Labiates, four thousand Rubiaceæ, three thousand Papilionaceæ, and thousands of Umbellifers, Rosaceæ, Crucifers, &c.; that, roughly speaking, two-thirds of Flowering Plants do not produce dust, it is evident that the term cannot have a general application. Consequently, Botanists speak of *Pollen* and not flower-dust. It is true this word simply means flour, and that its selection has not been a very happy one. Still the term has entered into botanical terminology, where it will remain. It is given to all those cells produced in the flowers of Phanerogams, which contain the spermatoplasm.

Pollen, then, consists of cells which contain spermatoplasm, and may be compared to the antheridia of Cryptogams. A definite portion of the substance of certain leaves of the floral axis is appropriated to the production of Pollen. These leaves, known as *Stamens*, resemble the other leaves of the floral axis in that they are inserted in whorls, or one above the other in a much-flattened spiral. Very few species of plants possess only a single stamen in each flower. The majority of flowers contain stamens arranged spirally or in whorls. As a rule stamens are inserted according to the $\frac{1}{3}$ or $\frac{2}{5}$ system (*cf.* vol. i. pp. 399, 400). In many cases their number and insertion resembles that of the petals and carpels of the same flower, though more frequently there is a difference. Thus, in the flowers of the Tulip-tree (*Liriodendron*), whilst the perianth-leaves have a divergence of $\frac{1}{3}$, the stamens are arranged according to the $\frac{1}{3}\frac{2}{4}$ system. In *Ranunculus* the leaves of the perianth are arranged on the $\frac{2}{5}$ plan, the stamens on the $\frac{8}{21}$; in *Polygonum* the former on the $\frac{1}{2}$, the latter on the $\frac{3}{8}$ system.

Since in every species of plant the number of stamens remains constant, thus in the Mare'stail (*Hippuris*) there is one, in Lilac two, in Iris three, in the Woodruff four, in the Violet five, and in the Tulip six stamens, their number has been made the basis of a classification of flowering plants at once convenient and popular, though not strictly scientific. In the well-known System of Linnæus plants are arranged into groups called Classes, in which the first class (*Monandria*) includes all forms with a single stamen, the second (*Diandria*) those with two stamens, and so on.

The aggregate of stamens in a flower is termed the *Andrœcium*. As a rule the

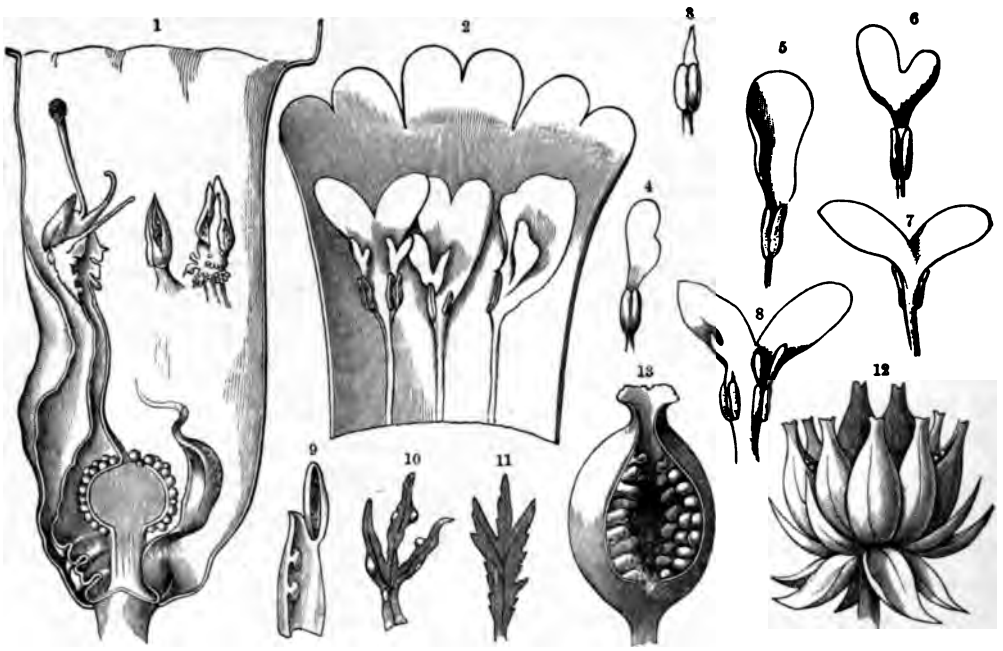

Fig. 213.—Stamens of double and monstrous flowers.

[1] Vertical section of a green flower of *Primula japonica*. [2] Vertical section of a double flower of *Primula spectabilis*. [3-8] Isolated stamens from the same flower. [9] Stamen from a green flower of the Tiger Lily (*Lilium tigrinum*). [10, 11] Foliaceous stamens from a flower of *Campanula Trachelium*. [12] Green flower of *Saxifraga stellaris*. [13] A single stamen from the same flower. (All the figures enlarged.)

andrœcium is inserted between the leaves of the perianth and the carpels, so that from without inwards the sequence is perianth, stamens, carpels. Sometimes the carpels are wanting, so that the stamens constitute the inmost members of the flower; similarly also carpels may be present but no stamens.

We distinguish in a stamen that portion which is concerned in the production of Pollen—the *Anther*—and its stalk, the *Filament*. The stamens in many flowers are partly metamorphosed into petals; indeed, there are grounds for believing that all petals have been originally modified from stamens. What are known as "double flowers" are often flowers in which the stamens have given place to petals. All intermediate stages between stamens and petals can be seen in double-flowered Roses, Carnations, and Primulas (*cf.* figs. 213 [3, 4, 5, 6, 7]). Not infrequently, at the

place where a petal narrows into its stalk or "claw", a little yellow swelling or callosity may be seen; this may be regarded as a reduced anther, and now and then it possesses the character of an anther, and contains actual pollen. It is frequently observed in double flowers that a multiplication of the leaf accompanies the con-

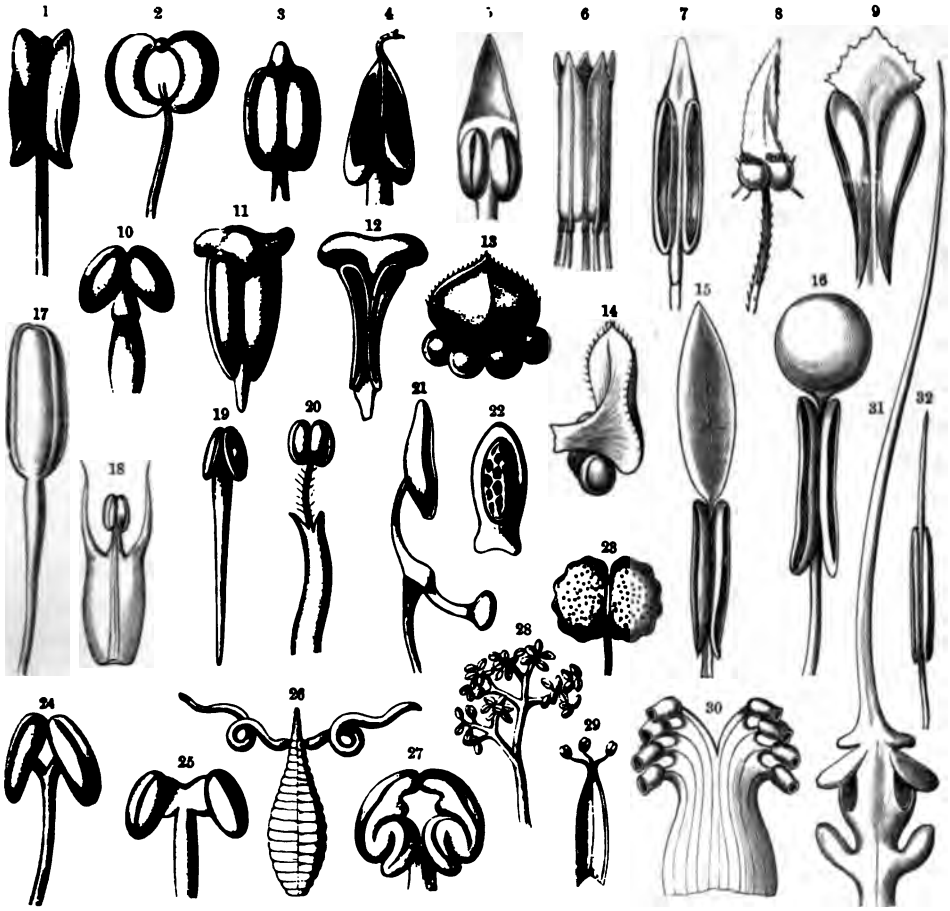

Fig. 214.—Stamens.

[1] *Empleurum serrulatum.* [2] *Hypericum olympicum.* [3] *Juglans regia.* [4] *Soldanella alpina.* [5] *Viola odorata.* [6, 7] *Artemisia Absynthium.* [8] *Haminia* (after Baillon). [9] *Abies excelsa.* [10] *Euphorbia canariensis.* [11, 12] *Platanus orientalis.* [13, 14] *Juniperus Sabina.* [15] *Halicnocnemis gibbosa.* [16] *Halantium Kulpianum.* [17] *Sanguinaria canadensis.* [18] *Allium sphærocephalum.* [19] *Actæa spicata.* [20] *Aconitum Napellus.* [21] *Salvia officinalis.* [22] *Viscum album.* [23] *Mirabilis Jalapa.* [24] *Tilia ulmifolia.* [25] *Thymus serpyllum.* [26] *Acalypha* (after Baillon). [27] *Bryonia dioica.* [28] *Ricinus communis.* [29] *Corydalis capnoides.* [30] *Polygala amara.* [31] *Doryphora* (after Baillon). [32] *Paris quadrifolia.* (All figures somewhat enlarged.)

version of stamens into petals. In the place of a single stamen we may find two stamens partially converted into petals, or there may be a greater number of petal-like leaves, standing one behind another, or, finally, we may have the appearance shown in figs. 213[2] and 213[3] of a double Primula.

By the action of parasitic Aphides and Insects stamens often assume a leaf-like appearance, they become green like the carpels described on p. 80. Such instances are of value in comparing the various parts of a stamen with those of the

hypothetic fundamental type of leaf-structure. At the first glance it might be supposed that the filament is a metamorphosed petiole, and the anther a metamorphosed lamina. But these monstrous flowers seem to indicate that such is comparatively rarely the case. Thus in the green stamens of *Campanula Trachelium* (figs. 213[10] and 213[11]) there are scattered everywhere over the green substance of the lamina yellow excrescences and warts containing reduced pollen-cells, and occasionally these occur fused together into actual portions of anthers; hence it may be inferred that in this case the anther may be regarded as equivalent to a green lamina. But far more frequently in such cases the pollen-producing tissue is found at the *base* of the lamina only, at the upper extremity of the leaf-stalk, where these two parts articulate. From this we may conclude that in the majority of cases anthers correspond to that portion of a leaf at which the stalk runs into the lamina. In such stamens the lamina is entirely suppressed, or is represented by a continuation above the pollen-producing region.

A few forms of this continuation above the anther, which we regard as representing a leaf lamina, are illustrated in fig. 214. Figs. 214[1] and 214[2] show it as a small shot-like grain, 214[3] as a truncate cone, 214[4] as a two-pronged fork, 214[5, 6, 7] as a flat, triangular scale, 214[8] as a toothed, sword-shaped process, 214[9, 11, 12, 13, 14] as a curved membraneous scale, 214[15] and 215[16] as a coloured bladder for attracting insects; and, finally, figs. 214[31] and 214[32] as a long, whip-like bristle.

That the filament of the stamen, or at any rate its lower portion, corresponds to a leaf-stalk seems so obvious, that it is hardly necessary to prove it by comparison with monstrous cases. Its name of *filament* indicates its character in a great number of flowers. Examples of these are Hemp, Hop, Wheat, Rye, Rice, Maize, Flax, and many others. For many cases no doubt the term filament is unsuited, as, for instance, in the thick, abbreviated stalks in the Violet and Bryony (figs. 214[5] and 214[27]). Similarly the filament may be strap-, spindle-, or club-shaped. The last is the case in *Thalictrum aquilegifolium*, *Bocconia*, *Sanguinaria*, and *Actæa spicata* (*cf.* figs. 214[17] and 214[19]), and it has been observed that the stamens very readily oscillate at the moment of liberation of pollen with the slightest breath of air. Like the foliage-leaves of the Orange, the stalks of which are provided with a peculiar joint, many Spurges and Labiates have hinged filaments (*cf.* figs. 214[10] and 214[21]). These hinges are wonderfully fashioned in many species of *Salvia*, reminding one of the articulation of the feet of insects; their importance in fertilization will be described in a later chapter. In the Linden the filament forks immediately below the anther (fig. 214[24]), whilst in *Corydalis* it is band-like, and divides into three (fig. 214[29]). In the Castor Oil Plant (*Ricinus*), and many other Euphorbiacæ, it is much divided and branched (fig. 214[28]). These *divided* filaments are not to be confused with *fused* ones, for occasionally we find that the filaments of adjacent stamens unite with one another into a ribbon or tube, as for instance in Mallows, Papilionaceæ, and Polygalaceæ (*cf.* 214[30]).

Attached to the sheath of foliage-leaves curious appendages, the stipules, are often found (*cf.* vol. i. p. 595). In the case of stamens these are but rarely met

with. They occur, however, in certain species of Ornithogalum (e.g. *Ornithogalum nutans* and *chloranthum*), in *Allium rotundum* and *sphærocephalum*, and in the Monkshood (*Aconitum*). Occasionally such staminal stipules are modified as honey-secreting glands at the base of the stamen, *e.g. Doryphora* (*cf.* figs. 214[18] and 214[20]).

It sometimes happens in monstrous flowers that the stamens are transformed into carpels, or we may find here and there an isolated stamen, which is partly so modified and partly still polliniferous. In such monstrosities it usually happens that it is the upper part which forms pollen, and the lower part which produces ovules (*cf.* figs. 213[1] and 213[9]). From this and other facts it has been inferred that the ovary corresponds really to the sheaths, the style to the petioles, and the stigma to the laminæ of the floral-leaves concerned. The monstrous flower of a Saxifrage (figs. 213[12] and 213[13]) shows that anthers and ovules can be produced from the same part of the leaf-stalk. This flower (213[12]) produces at the periphery five sepals and five narrow, green petals; in the centre two carpels (shaded dark in fig. 213[12]) as in normal Saxifrage flowers. Between the petals and carpels, *i.e.* where the stamens are usually found, there are ten structures which, whilst resembling both carpels and stamens to some extent, remind one forcibly of the excavated leaf-rachis of so many of the Pitcher Plants (*cf.* vol. i. pp. 125–133.) One of these is represented in fig. 213[13]. Its free extremity consists of an irregularly serrated scale, which may be compared either to a stigma or to the continuation of an anther, and may be regarded as the metamorphosed lamina. The excavated portion below may be regarded as the petiole. In its cavity are four rows of yellow protuberances, which might at first sight be taken for ovules. Closer investigation shows, however, that they contain pollen-mother-cells, each inclosing four pollen-grains. Here, then, we find the petiole consisting partly of carpel and partly of anthers, from which it may be concluded that that portion of the carpel which produces ovules corresponds entirely in position to the pollen-producing tissue.

The parts of the anther which produce Pollen in special chambers are known as *Pollen-sacs*, the tissue which binds these together as the *connective*. The connective is a direct continuation of the filament, and, like this, is penetrated by a vascular bundle. The pollen-sacs may be arranged like niches around the columnar connective, which itself terminates in a sort of little shield, as in the Yew Tree (*cf.* fig. 234[2]), or they may be situated symmetrically right and left of it. In the latter case the pollen-sacs may lie at the edge of the connective in one place, as in the Juniper (figs. 214[13] and 214[14]), or they may be in pairs, *i.e.* two pollen-sacs to the right and two to the left of the connective (fig. 214[3]). This latter form is by far the most frequent, and occurs in certainly 90 per cent of all Phanerogams. It must be pointed out that the two pollen-sacs of each pair are separated from one another by a partition-wall only in the young anther. This disappears later on, and in the mature anther one finds, instead of four, only two sacs filled with pollen. Sometimes all four pollen-sacs run together in this way, by the breaking down of the parti-walls, as in Sundew (*Drosera*), Moschatel (*Adoxa*), *Monotropa*, and especially in *Globularia* (*cf.* figs. 216[27] and 216[28]). In

Orchids, on the other hand, the number of pollen-sacs is reduced to two, a number which remains unaltered at maturity.

The pollen-sacs in the anthers of the Mimoseæ are very curiously formed. In the anthers of *Acacia*, *Albizzia*, *Calliandra*, and *Inga*, there are eight spherical chambers in which pollen is produced, whilst in *Parkia* we find longitudinal rows of lenticular cavities in which balls of pollen lie embedded. The anthers also of the Rhizophoreæ show several longitudinal rows of such chambers, amounting in all to as many as thirty. The anthers of the Mistletoe (*Viscum*, fig. 214 [22]) contain as many as forty to fifty pollen-chambers. In the majority of the Laurels (Lauraceæ) each anther is divided into four cavities, which stand in pairs, one above the other. As a rule, all four open towards that side by which insects visiting the flower for honey have to pass.

Many marked variations in the form of the anther are due to the relative dimensions of connective and pollen-sacs. Thus in the majority of Ranunculaceæ, Magnoliaceæ, Nymphæaceæ, and Papaveraceæ, the connective is broad, the pollen-sacs forming only a narrow rim to the anther (*cf.* fig. 214 [17]). In the Skull-cap (*Scutellaria*), Calamint (*Calamintha*), Thyme (*Thymus*), and many other Labiates, as also in several Rosaceæ (*Rosa*, *Agrimonia*, &c.), the connective has the form of a three- to six-sided mass of tissue in which are embedded the spherical or egg-shaped pollen-sacs. Such anthers frequently resemble an insect's head with two lateral eyes. It is not always possible to distinguish the limits of connective and filament, the whole stamen resembling a truncate column or anvil (figs. 216 [26] and 216 [32]).

Fig. 215.—Curved anthers in the flower of *Phyllanthus Cyclanthera* (after Baillon).

Sometimes the connective assumes the form of a bar or lever running transversely to the filament, to which it is attached by a movable joint. This is notably the case in certain species of *Salvia*, to be described hereafter. Such a connective moves very readily upon its fulcrum. In many Liliaceæ (*e.g.* Tulips, Lilies, and Crown Imperials) and several Gentians (*Gentiana ciliata*, *nana*, &c.), the anther is united with the filament by an extremely delicate joint, so that the slightest touch sets it in vibration (versatile anthers). As examples of bulky pollen-sacs and much reduced connective, *Mirabilis Jalapa* (fig. 214 [23]) and *Solanum Lycopersicum* (fig. 216 [2]) may be quoted as examples.

It stands to reason that the character of the anther, indeed of the whole stamen, is correlated with the form of the pollen-sacs. All possible stages occur between globular and egg-shaped, and between egg-shaped and linear pollen-sacs. The drawings of sixty-four different stamens in figs. 214 and 216 give a good idea of the variety in this respect. Very curious are the curved anthers of *Phyllanthus Cyclanthera* (fig. 215), and those of *Acalypha*, which resemble a ram's horns (fig. 214 [26]); the same remark applies to the undulating anthers of many Cucurbitaceæ, of which those of *Bryonia dioica* may serve as an example

(fig. 214[27]). There are forms allied to this last-named plant in which the anthers show very complicated convolutions—like those of the human brain.

When the time draws near for the pollen to leave its place of origin, its cells —whether in a loose powder or sticking one to another—become free from the inclosing wall of the anther, and lie embedded in the cavity of the pollen-sac, as it were in a purse or pocket, awaiting their release. The pollen-sac, hitherto

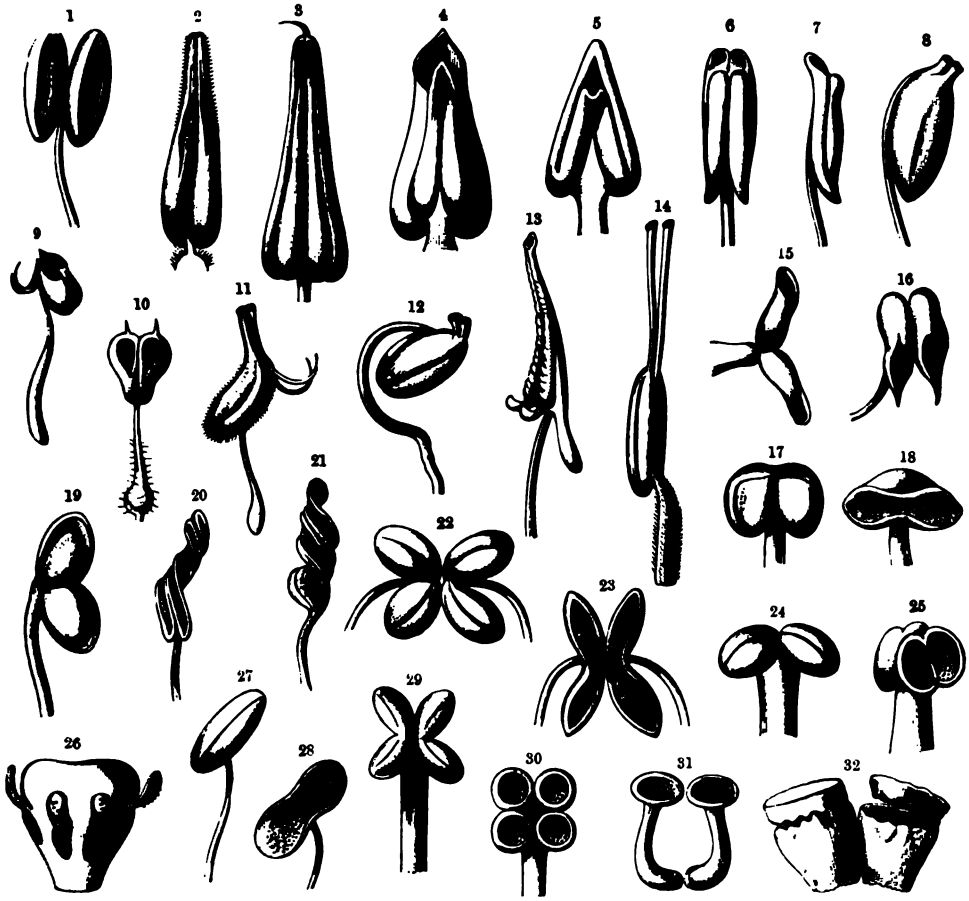

Fig. 216.—Stamens.

[1] *Calandrinia compressa.* [2] *Solanum Lycopersicum.* [3] *Galanthus nivalis.* [4] *Cyclamen europæum.* [5] *Ramondia pyrenaica.* [6, 7] *Cassia lenitiva.* [8] *Pyrola rotundifolia.* [9] *Arctostaphylos Uva-ursi.* [10] *Arctostaphylos alpina.* [11] *Vaccinium uliginosum.* [12] *Pyrola uniflora.* [13] *Medinilla* (after Baillon). [14] *Vaccinium oxycoccus.* [15] *Calceolaria Pavonii.* [16] *Tozzia alpina.* [17, 18] *Sibbaldia procumbens.* [19] *Galeopsis angustifolia.* [20, 21] *Erythræa Centaurium.* [22, 23] *Melissa officinalis.* [24, 25] *Calla palustris.* [26] *Nyctandra* (after Baillon). [27, 28] *Globularia cordifolia.* [29, 30] *Theobroma Cacao.* [31] *Pinguicula vulgaris.* [32] *Garcinia.* (All somewhat enlarged.)

closed, now opens, and the pollen is liberated. This opening or *dehiscence* of the pollen-sacs is accomplished in various ways. It has been already explained that most young anthers contain four sacs which rarely all remain distinct, but, by the breaking down of the parti-walls between each pair, become merged into two cavities.

These two cavities may be spoken of as anther-halves. In cases where the

four cavities remain distinct, a curious aperture is formed above each of them, as, for instance, in *Theobroma Cacao* (figs. 216[29] and 216[30]). When, however, the aforesaid fusion takes place (e.g. *Calla palustris*, figs. 216[24] and 216[25]), two openings only are formed. The anthers of *Globularia* have a very small punctiform connective and four pollen-sacs joined into an ellipsoidal body. After the disappearance of the parti-walls, leaving a single cavity occupied by pollen, a gaping, transverse slit arises, so that the anther is transformed into an open vessel (*cf.* figs. 216[27] and 216[28]). After the removal of the pollen the remains of the original parti-walls can be distinguished as two intersecting ridges. Similarly in the Butterwort (*Pinguicula*, fig. 216[31]) and in the majority of so-called one-celled anthers. In many Labiates, in which the anthers of adjacent stamens are in contact, and to some extent united together (syngenesious), the openings of the pollen-sacs in each anther unite, with the result that a pair of somewhat sinuous niches are presented, borne on the two curved filaments (*cf.* figs. 216[22] and 216[23]).

Dehiscence is accomplished sometimes by the formation of holes or pores, sometimes by slits. Of anthers with *porous dehiscence*, the greatest variety is exhibited by the Heath tribe and Pyrolaceæ. In the anthers of the Bilberry, Bog Vaccinium, Cowberry, and Cranberry (*Vaccinium Myrtillus, uliginosum, Vitis-idæa, Oxycoccos*), as also in Winter-green (*Pyrola*), the pouch-like pollen-sacs are drawn out into shorter or longer tubes, each of these tubes opening at its extremity by small circular pores (*cf.* figs. 216[8, 11, 12, 14]). But much more frequent is a dehiscence by means of *slits*. These are either longitudinal or transverse, or they may be sinuous or semicircular. When they are semicircular a valve or trap-door is cut out of the anther-wall.

At its first formation the slit resembles one cut by a sharp knife (*cf.* fig. 216[1]). In a number of cases the margins of the slit remain together, so that the aperture retains the form of a narrow crack; more frequently, however, the slit gapes, its margins roll up outwards or are folded back like a lid or folding-door. The *longitudinal slits* reach from end to end of the pollen-sacs (fig. 216[1]), or they may take the form of short gaping clefts near the free extremity of the anther. In the latter case (several examples of which are represented in figs. 216[2, 3, 6, 7, 9, 10, 13, 15, 16]), the slits very much resemble pores, from which they can only be distinguished in some cases by their mode of development. Occasionally the short, gaping clefts of adjacent anther-halves unite into a single opening, with a heart-shaped or rhomboidal outline, by which the whole of the pollen of both anther-halves escapes (examples are *Cyclamen* and *Ramondia*, figs. 216[4] and 216[5]). *Transverse slits* are met with most frequently in the stamens of Euphorbiaceæ, Cyclanthaceæ; also in a few Rosaceæ (*Alchemilla* and *Sibbaldia*, figs. 216[17] and 216[18]), in the Golden Saxifrage and Moschatel (*Chrysosplenium* and *Adoxa*), in *Globularia*, *Malva*, and others. On the whole, however, this method of dehiscence is rare. Of still rarer occurrence is that form of dehiscence in which semicircular slits arise in the anther-wall, producing valves or trap-

doors. This is known as *valvate dehiscence*. It is met with generally in Berberidaceæ (e.g. *Berberis* and *Epimedium*) and Lauraceæ. In the Bay Laurel, Camphor, and Cinnamon Trees (*Laurus nobilis, Camphora officinalis*, and *Cinnamomum*) and *Nyctandra* (fig. 216 [26]) are found little apertures on one side of the stamen, each with its trap-door or valve, which is raised up in dry, but shut down in wet weather. The anthers of *Mimulus, Galeopsis*, and *Garcinia* (figs. 216 [19] and 216 [32]) resemble little tubs or boxes, which on opening raise their lid-like valves.

The dehiscence of the anthers in many plants is accompanied by yet other changes. The two anther-halves may become partly separated from their attachments and become twisted or diverge at right angles. If the anther-halves separate at the base only, as in *Convolvulus, Gentiana*, and *Menyanthes*, the anther assumes the form of an arrow-head; if they separate both above and below, and at the same time become somewhat bent, we have an X-shaped anther, found in many Grasses. In many Crucifers (*Diplotaxis, Sinapis*, &c.) the anthers become spirally twisted after dehiscence, a feature very pronounced in the Centaury (*Erythræa*, figs. 216 [20] and 216 [21]). A very striking phenomenon is the shortening which not a few anthers with longitudinal slits undergo after dehiscence. The anthers of most Liliaceous plants are long and linear; they dehisce by means of slits from above downwards. In the course of a few hours they are transformed into globular bodies, covered with pollen. In *Gagea lutea* these balls have a diameter only one-third of the previous length of the anther, whilst the anthers of the Crown Imperial (*Fritillaria imperialis*) shorten from 20 to 10, those of *Narcissus poeticus* from 11 to 4, and those of *Scilla bifolia* from 2 to 1 millimetres.

Each one of the various occurrences which accompany or succeed dehiscence depends upon some structural character of the anther-wall. The relations are simplest in those anthers which open by means of pores. The pores arise from the absorption of limited portions of the wall. Further changes, such as the shrivelling or shortening of the anther, or the expanding of the apertures, do not occur. There is a corresponding simplicity of the tissues of the anther-wall. Similarly, in anthers (*e.g.* Orchids) in which a splitting arises along a previously-indicated line, or in consequence of the absorption of a row of cells, no peculiarities are noticeable on the wall. But where slits with movable lips and valves are developed, cells of characteristic structure are present, which may be termed the contractile cells. One series consists of more or less cubical cells, and exhibit, on portions of their walls, fibrous or rod-shaped thickenings. The wall of one of these cells directed towards the cavity of the anther is equally thickened, that towards the outside is thin and delicate, easily folded, and destitute of thickenings. The side-walls, however, are characteristically strengthened by rod-like thickenings, which in their distribution may be compared to a hand, in the position usually employed in grasping an apple; the palm corresponds to the strongly-thickened inner wall, and the fingers to the tapering, rod-like thickenings of the

side-walls. As the cells dry a contraction of the rod-like thickenings supervenes, leading to a movement like that of the afore-mentioned hand when the tips of the fingers approach one another. Simultaneously the thin outer walls are thrown into folds, so that where a number of these cells are present, side by side, the whole outer surface will contract. These cells, being appropriately distributed over the wall of the anther, will cause the slit-margins to fold back or the valves to be raised. Besides these, other forms of contractile cells are present, differing from those described chiefly in form rather than in their mode of action.

It must suffice here to mention only a very few instances. The anther-wall in Conifers consists of a single layer of contractile cells, whilst that of *Agave* reaches the other extreme, there being six to eight layers of such cells present. As a rule the contractile layer is covered externally by a layer of delicate, thin-walled cells, known as the *Exothecium*; the contractile layer constitutes the *Endothecium*. The lining of the pollen-chambers consists of yet a third layer, the *tapetal cells*. In anthers which have dehisced this last-mentioned layer is rarely demonstrable, it having been already absorbed. Of the various layers it is the middle one, the endothecium (contractile cells), which is active in the various movements under discussion.

In the discharge of the pollen from the opened anthers a great variety of methods prevails. In the Nettle and Mulberry the filament of the stamen uncoils like a spring at the moment of dehiscence of the anther, and the pollen is forcibly scattered (fig. 229). The whole event is instantaneous, and to the observer resembles an explosion. In other plants dehiscence is accomplished quietly, and the pollen, which escapes slowly, may be first of all stored up temporarily at definite spots within the limits of the flower. This storage occurs a good deal more frequently than is generally supposed, and stands in relation to various events which will be fully discussed later on. In Papilionaceæ the liberated pollen is deposited in the hollowed apex of the *Keel*; in the Violet it is stored in the grooves of the lowest, spurred petal; in the Poppies, Roses, and Buttercups, it falls, at any rate in part, on to saucer-like depressions of the petals. The dust-like pollen as it falls from the anthers of the catkins of the Walnut, Hazel, Birch, and Alder, is received temporarily on the upwardly-directed under-surfaces of the flowers standing below (*cf.* fig. on p. 742, vol. i.). In Composites, Campanulas, and several Stellatæ, the pollen is stored on the style or stigma, but not, as was previously supposed, upon the receptive portions of this organ. On the contrary, it is retained here by various hairs and papillæ, specially designed for the purpose. Then, in the Proteaceæ again, the pollen is deposited, whilst the flower is still in bud, upon the summit of the stigma, without, however, coming into contact with the receptive spot; the stigma in this case serves, at the commencement of flowering, as a temporary depôt for the pollen. In Sarracenia the pollen falls upon the stigma, which has the form of an expanded umbrella, and here for a while it remains, but not in contact with the receptive points. We shall hardly overstep the mark in saying that in some 20,000 species of plants

the pollen is temporarily stored in some portion of the flower and preserved for future use.

More frequently, however, the pollen remains within the opened anther. Usually these flowers are visited by insects which disturb the anthers and release the pollen, or they dust themselves over with it and carry it off to another flower.

The fact that the anthers are directed sometimes inwards, sometimes outwards, is correlated with these insect-visits. Where the slits or pores of the anthers are directed towards the periphery of the flower, one speaks of outwardly-directed anthers (extrorse), where toward the centre of the flower, of inwardly-directed (introrse). These relations are of importance in respect of insect-visits. If the honey is situated outside the whorl of stamens, the insects must pass between the stamens and petals to secure the nectar, as in *Colchicum*, *Iris*, *Convolvulus*, *Epimedium*, and *Laurus*. Here it will be advantageous for the anthers to be extrorse. On the contrary, when the honey is between the ovary and the bases of the stamens, and the insects have to penetrate to this region, as in Gentians and Opuntias, the stamens will be introrse. It is of great importance that the pollen exposed in the anthers should be rubbed off by the insects and carried to other flowers, a result only obtainable when the dehiscent side of the anther is placed in the way of the insect as it enters or leaves the flower.

Numerous other peculiarities affecting the structure, position, and movements of stamens will be dealt with later on, when treating of the removal of pollen from and to flowers by insects and other animals.

POLLEN.

Like all other leaf-structures, stamens arise in the first instance as convex projections from their points of insertion on the stem. These projections consist of a homogeneous, small-celled tissue. They soon, however, assume a club-shaped form, and the outlines of anther and filament become recognizable. A vascular bundle is found traversing the entire length of each stamen, and the anther, which increases in size more rapidly than the filament, shows symmetrically-arranged, longitudinal grooves, with projecting portions between, arranged in pairs. The cells situated immediately below the surface of the young anthers become now marked out into tissues of two kinds. Towards the outside three layers of cells become distinguishable, and these, with the outermost, enveloping layer give rise to the wall of the anther; within, large cells become conspicuous, and form what is known as the *archesporium*.

These archesporial cells are arranged either in nests or in longitudinal rows embedded in the surrounding tissue. In the latter, the more usual, case, there are four, rarely two or eight, such rows arranged in pairs right and left of the central vascular bundle. Although at this stage of development all the cells of the anther hang together into a continuous mass, the existence of the future pollen-sacs—now

filled with the archesporial cells—is easily recognized. As time goes on the contrast between the wall of the anther and the contents of the chambers becomes more pronounced. The archesporial cells divide, giving rise to the pollen-mother-cells which entirely fill the pollen-sacs. Of the layers of the anther-wall, the inmost is usually dissolved, so that the mother-cells are bathed in a fluid mucilage; thus the wall comes to consist solely of the outmost, enveloping layer and of the contractile cells ("fibrous layer") within.

Changes continue in the chambers or pollen-sacs, and in the partition-walls between them. The walls of the pollen-mother-cells become thickened, and often show a stratification. The protoplasm within divides into four parts, arranged frequently, though not invariably, in the corners of a 4-sided pyramid (*i.e.* in tetrads). Each of these cells becomes invested with a wall of its own, at first thin and delicate, but afterwards thickened and stratified. These are the pollen-grains. Their protoplasm possesses the property of a fertilizing agent, and is termed the *Spermatoplasm*.

In most plants a further division of the protoplasm in the pollen-cells takes place. This is conspicuous in the Conifers and Cycads, but relatively obscure in the majority of flowering plants. Of the two or more cells thus arising within the pollen-grain one only takes an actual part in fertilization.

How long the spermatoplasm retains its fertilizing properties unimpaired has not been sufficiently investigated. It has been stated of the plants enumerated below that this property is lost as follows:—

In *Hibiscus Trionum*	after 3 days.	In the Larger Periwinkle (*Vinca major*)	after 43 days.
„ The Wallflower (*Cheiranthus Cheiri*)	„ 14 „	„ *Pæonia pubens*	„ 58 „
„ „ Pansy (*Viola tricolor*) ...	„ 26 „	„ *Pæonia tenuifolia* ...	„ 65 „
„ „ Bugle (*Ajuga reptans*) ...	„ 32 „	„ *Clivia nobilis*	„ 76 „

It is by no means an unusual thing for gardeners to send the pollen of Cycads and Palms for fertilization to distant countries without its properties being impaired, provided it is kept dry during transit. The Arabs, who artificially pollinate the female flowers of the Date-palm, put aside some of the pollen from year to year, so that, in the possible event of the male flowers not developing, they may ensure a crop of dates. According to tradition, the pollen of Date-palms, Hemp, and Maize, can be used effectively for artificial pollination even after a lapse of eighteen years. Unfortunately, reliable investigations are wanting to show whether these accounts belong to the realm of gardeners' stories or not.

A great diversity obtains as to the manner of coherence of the pollen. When the walls of the mother-cells, containing the pollen-grains, become entirely absorbed, the pollen-sacs are filled with isolated cells, a condition which may be described as *free pollen*. Even now numbers of adjacent pollen-grains may cohere in clusters, in consequence of their possessing sticky coats or other arrangements. But in this case there is no suggestion of its being a real tissue, a difference of some moment.

In many plants, on the other hand, the pollen-cells remain, as they arose in the

mother-cells, united together in fours, and in this condition they leave the anther-cavities. These little pollen-aggregates are termed *tetrads*. Examples of such plants are:—the Ericaceæ (*Erica, Calluna, Menziesia, Andromeda*), the Bearberry (*Arctostaphylos*), the Strawberry Tree (*Arbutus*), the Alpine Rose (*Rhododendron*), *Ledum, Kalmia*, the Cranberry and Bilberry (*Vaccinium*); the Epacridaceæ, *Epacris* and *Leucopogon*; many Winter-greens (Pyrolaceæ); a few Sedges (*Juncus Jacquinii* and *Luzula vernalis*); finally *Anona, Drimys, Jussieua*. In the plants just enumerated the tetrads correspond to the four pollen-cells in the corners of the mother-cell (*cf.* fig. 219 [2]); but in the Apocynaceæ (*Apocynum, Periploca*), in numerous Orchids (*Ophrys, Spiranthes*), in *Fourcroya* (nearly related to *Agave*), and in several Bulrushes (*Typha Shuttleworthii* and *latifolia*), the four pollen-cells are arranged in one plane. In a few Willow-herbs (*e.g. Epilobium montanum* and *hirsutum*) the four cells are joined, but so slightly that they are readily separated on pressure.

Of much rarer occurrence than tetrads are *pollinia*. This name is given to the resultant mass of pollen-cells, when the whole of the pollen produced from a single archesporium (*i.e.* the whole contents of a pollen-sac) remain joined together into a tissue. A pollinium may consist of 8, 12, 64, or even many hundreds of pollen-cells. In the Mimoseæ the pollinia, which are found serially arranged, are lenticular, egg-shaped, or globular in form; in the Asclepiads they are spatulate, and consist of hundreds of pollen-cells. The pollen-masses of many Orchids are built up of numerous little clusters of pollen-cells, and show a branching or lobing; each of these clusters or lobes consists of greater or smaller pollinia. The masses, into which the pollinia of Orchids are aggregated, usually terminate in a stalk which is attached at its other end to a disc. This disc is so sticky that it readily adheres to any object coming in contact with it—a fact of significance in the conveyance of the pollinia from flower to flower by insects.

The dimensions of pollen-grains are very various in different groups of plants. Thus, whilst in the Forget-me-not (*Myosotis*), Borage (*Borago*), Comfrey (*Symphytum*), and Boragineæ generally, as also in Artocarpeæ (e.g. *Ficus*), the pollen-grains are very small, in Cannaceæ, Malvaceæ, Cucurbitaceæ, and Nyctagineæ, they are relatively large. The following table of diameters of pollen-grains shows the variation which exists in this respect:—

	Millimetres.		Millimetres.
Myosotis alpestris, ...	0·0025–0·0034	*Viola tricolor*, ...	0·062–0·071
Lithospermum affine, ...	0·0042–0·0052	*Convolvulus sepium*, ...	0·076–0·084
Ficus pumila, ...	0·0045–0·0056	*Geranium Robertianum*, ...	0·085–0·094
Carinthe minor, ...	0·0050–0·0057	*Opuntia cynanchica*, ...	0·15 –0·20
Echium vulgare, ...	0·010 –0·014	*Oxybaphus nyctagineus*, ...	0·18 –0·22
Pilea microphylla, ...	0·018 –0·020	*Morina Persica*, ...	0·19 –0·24
Rhamnus cathartica, ...	0·022 –0·032	*Cucurbita Pepo*, ...	0·20 –0·23
Syringa vulgaris, ...	0·024 –0·034	*Mirabilis longiflora*, ...	0·20 –0·24
Aloe denticulata, ...	0·035 –0·050	*Cucumis Melo*, ...	0·20 –0·24
Yucca angustifolia, ...	0·055 –0·065	*Mirabilis Jalapa*, ...	0·22 –0·25

The pollen-grains of the Marvel of Peru (*Mirabilis Jalapa*) are consequently

a hundred times greater than those of the Alpine Forget-me-not (*Myosotis alpestris*). It appears also that in many flowers which remain open but a single day or night, as, for instance, the Gourd and Melon, *Portulaca*, *Morina*, and the various species of *Mirabilis*, the pollen-grains are especially big. In a single anther-cavity of *Mirabilis Jalapa* there are, on the average, 32, and in one of *Borago officinalis* 60,000 pollen-grains.

In form pollen-grains are generally ellipsoidal (*cf.* figs. 217 [13] and 217 [14]), at

Fig. 217.—Pollen-grains.

[1] *Cobæa scandens.* [2] *Morina Persica.* [3] *Cucurbita Pepo.* [4] *Passiflora Kermesina.* [5] *Circæa alpina.* [6] *Convolvulus sepium.* [7] *Cannabis sativa.* [8] *Pinus Pumilio.* [9] *Mimulus moschatus.* [10] *Albucca minor* (dry and moistened). [11] *Dianthus Carthusianorum.* [12] *Corydalis lutea.* [13] *Gentiana rhætica.* [14] *Salvia glutinosa.* [1-3] ×80-90; [4, 5, 7, 8, 10] ×120-150; [11, 12] ×180; [6, 9, 13, 14] ×220-250.

any rate in quite half of all flowering plants. More rarely are they spherical (figs. 217 [1, 3, 4, 6, 7]). In the liliaceous *Tritelia* they are narrow and lancet-shaped, and in *Morina* (fig. 217 [2]) biscuit-shaped. In the Pine the pollen-grain possesses two hemispherical bladders, and resembles an insect's head with two huge eyes (fig. 217 [8]). In *Crucianella latifolia* they are barrel-shaped, and in *Brugmansia arborea* shortly cylindrical. Next to the ellipsoidal form, the angular or crystalline is the commonest. Thus the pollen-grains of the Nasturtium (*Tropæolum*) are 3-sided prisms, those of the Pansy (*Viola tricolor*) 4 or 5-sided, and those of Lady's

fingers (*Anthyllis vulneraria*) short 6-sided prisms with striated angles. A cubical form obtains in the pollen-grains of *Triopteris brachypteris* and *Basella alba*, that of a pentagonal dodecahedron in *Banisteria*, *Rivina*, and, in particular, in a number of Caryophyllaceæ, e.g. *Arenaria*, *Silene* and *Dianthus* (*cf.* fig. 217[11]). In the Dandelion (*Taraxacum officinale*), and in *Corydalis lutea* many crystalline forms occur, side by side, in the same anther (*cf.* figs. 217[12] and 218[4]). The tetrahedron, also, is not infrequently met with. This form occurs in *Thesium*, *Cuphea*, many Proteaceæ and Composites, sometimes with flat, sometimes with curved surfaces (*cf.* fig. 218[6]). A form, made up as it were of two spherical triangles joined together, occurs in *Circæa* and many other Onagraceæ (fig. 217[5]).

The above paragraph relates solely to the varieties in form of dry pollen-grains. In the great majority of cases the grains are variously striated and grooved. In ellipsoidal and spherical grains, the grooves run like meridian-lines, so that two

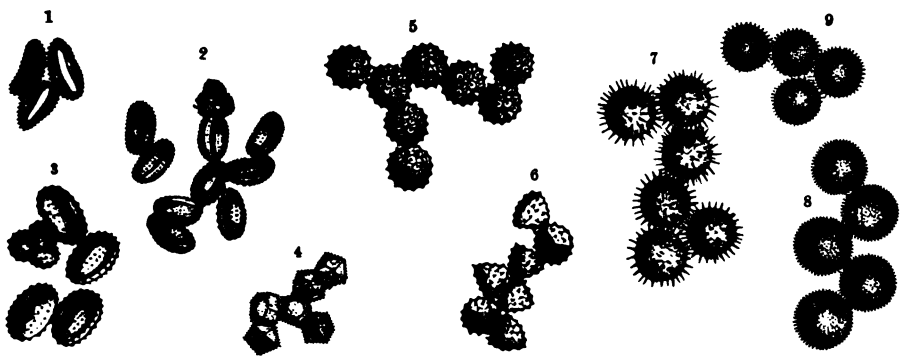

Fig. 218.—Pollen-grains.

[1] *Nymphæa alba.* [2] *Viscum album.* [3] *Carlina acaulis.* [4] *Taraxacum officinale.* [5] *Cirsium nemorale.* [6] *Buphthalmum grandiflorum.* [7] *Hibiscus ternatus.* [8] *Malva rotundifolia.* [9] *Campanula persicifolia*; ×200.

poles are distinguishable. The number of the grooves is constant for a given species, and even for whole families of plants. A single furrow is characteristic of the grains of the Tulip-tree, Magnolias, and Water Lilies (fig. 218[1]), of the Meadow Saffron, Tulip, Lily, Iris, Narcissus, and Snowdrop, of Palms, Grasses, and, indeed, Monocotyledons generally. Two furrows are found on the pollen-grains of *Calycanthus*, several climbing Smilacineæ (*Tamus*, *Dioscorea*), and several species of *Amaryllis*. A very great number of plants have three grooves, *e.g.* Rock-roses, Violets, Poppies, Ranunculaceæ, Roses, Almonds, many Papilionaceæ, Beeches, Oaks, and Willows, Solanaceæ, Gentians, Scrophulariaceæ, and many Composites (*cf.* figs. 217[13] and 218[8]). Four grooves have been noticed in several Boragineæ (*Anchusa*, *Nonnea*), some Labiates (*Teucrium montanum*, *Sideritis scordioides*), in *Houstonia*, *Platonia*, *Blackwellia* and *Cedrela odorata*; six in most Labiates (fig. 217[14]), nine or ten in *Sherardia*, *Borago*, and *Symphytum*; twelve in *Crucianella latifolia*; sixteen in *Polygala chamæbuxus*; twenty-one to twenty-three in *Polygala myrtifolia*. On crystal-like pollen-grains the grooves are extremely delicate, and their number depends on the number of angular ridges.

A very conspicuous feature of many pollen-grains is the infinitely varied sculpturing, &c., of their walls. Sometimes this takes the form of a delicate dotting of the wall, as in *Asarum*, Meadow Saffron, Rue, Salvia, Gentians, and Euphorbias, many Aroids and Musaceæ (*cf.* figs. 217 [13] and 217 [14]); or the projecting ridges may be transversely striated as in *Saxifraga aizoides*; or, again, delicate striations may run in meridian-like circles (e.g. *Brugmansia arborea*). Sometimes dotted lines are found arranged in various ornamental reticulating patterns. On the smooth surface of the grains of *Thesium alpinum* and *rostratum* reticulations occur, and in the centre of each mesh a distinct dot. Similiarly in Thrift and Sea Lavender (*Armeria* and *Statice*), and in the Corn Cockle (*Agrostemma Githago*). Often the surface presents considerable unevenness. In *Cuphea platycentra* the outer coat is prettily ridged, whilst in many other cases it is finely granulated. The little projecting granules may be either scattered equally over the whole surface, or they may be arranged in networks—which is specially the case in Cruciferæ (*Capsella, Raphanus, Sinapis*). In the Passion Flowers (e.g. *Passiflora Kermesina*, fig. 217 [4]) these networks are inclosed in shallow, ring-like depressions, whilst in *Cobæa scandens* (fig. 217 [1]) the surface has a honey-combed appearance. Sometimes the whole surface is dotted over with little wart-like projections, as in *Centaurea Jacea*, Mistletoe (*Viscum album*), White Water Lily (*Nymphæa alba*), and the tropical Bauhinias (*Bauhinia armata, furcata, cf.* figs. 218 [1] and 218 [2]); or it may be covered with sharp, needle-like prickles, as in the pollen-grains of Composites, Scabiouses, Campanulas, Cucurbitaceæ, Malvaceæ; also in the genera *Armeria, Amaryllis, Canna, Lonicera, Ipomœa*, and *Convolvulus* (*cf.* figs. 218 [3] and 218 [9]).

It is only the superficial layer of the pollen-grain which shows these sculpturings and projections, the inner layer, which abuts immediately upon the protoplasm, is homogeneous. The wall of pollen-grains is, as a rule, three-layered. These three layers are:—the internal one or *intine*, the middle one or *extine*, and the external one or *perine*. The extine and intine arise from the protoplasm of the pollen-cell itself; the perine, on the other hand, is deposited from the matrix in which the young pollen-grains lie embedded. It comes about in this way. The young grains first clothe themselves with delicate walls, which are in due time thickened. This is the extine. Within this they form a second layer, the intine. Lastly, the perine is deposited upon them from without. The intine and extine can generally be readily distinguished as separate layers, but between the extine and perine the boundary is by no means so well marked. The various sculpturings, prickles, and other unevennesses of the outer coat really appertain to the perine.

It sometimes happens at definite spots on the wall of a pollen-grain, from a separation of the molecules there, that little spaces or actual canals arise which open externally by tiny pores. This may be well observed in *Thesium, Prunella, Ipomœa*, and *Gentiana*. In these canals a yellow (rarely colourless) oil is contained, which oozes out in the form of minute drops when the grains are moistened and absorb water. Such at any rate is the behaviour in *Prunella grandiflora* and *Gentiana ciliata*. In many other plants the whole surface of the grain is saturated

with this oil. I ascertained that in about 400 out of 520 species investigated by me the outer surface was overlaid with oil. The layer is so thin that with dry pollen-grains it is not visible, but when they are placed in water, the coating is resolved into a number of minute, strongly-refringent droplets, which adhere to the swollen pollen-grains like tiny beads. There is no doubt that this coat consists of a fatty oil, since it is soluble in alcohol and olive-oil, and with osmic acid it turns dark-coloured and becomes congealed.

More rarely are pollen-grains found with masses of a sticky, structureless substance adhering to them. This substance does not form droplets with water, nor does it dissolve in alcohol and olive-oil. It may be termed *Viscin*, from the similarity which it presents tc the bird-lime obtained from the berries of the

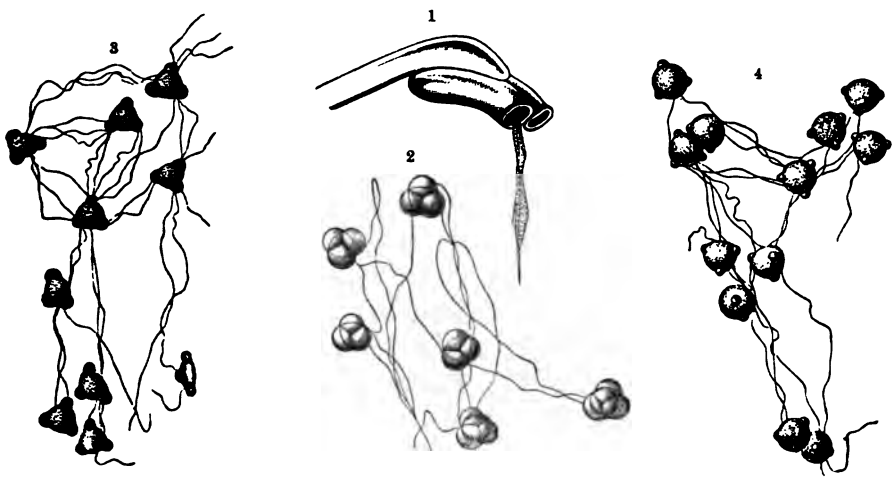

Fig. 219.—Pollen-grains and pollen-tetrads united by threads of viscin.
1, 2 *Rhododendron hirsutum.* 3 *Œnothera biennis.* 4 *Epilobium angustifolium.* 1×8; 2-4×50.

Mistletoe (*Viscum*). Such a viscin is met with on the surface of the pollen-grains of *Fuchsia, Clarkia, Circœa, Gaura, Godetia, Œnothera, Epilobium* — indeed, throughout Onagraceæ and in Azaleas, Rhododendrons, Orchids, and Asclepiads. It is very sticky, and on the slightest touch can be drawn out into delicate threads. The contents of the anthers, as they escape, in the Evening Primrose (*Œnothera*) and Willow-herb (*Epilobium angustifolium*) resemble fringes and tattered ribbons, or a broken net hanging from the adjacent anthers. Under the microscope this substance is seen to consist of pollen-grains, joined together by the sticky strings of viscin (fig. 219 [3] and 219 [4]). The phenomenon is even more striking in the numerous species of *Rhododendron*. In *Rhododendron hirsutum* all the pollen-tetrads of an anther-cavity are held together by a mass of sticky viscin. The anther dehisces by two terminal pores, and from these the pollen-tetrads ooze out to some extent. If the sticky mass be touched with a bristle it adheres, and the whole contents of the anther can be readily withdrawn (fig. 219 [1]). Its appearance under the microscope is shown in fig. 219 [2]. In many species, as for instance in the elegant *Rhododendron Chamæcistus* of the Northern Limestone Alps, and in the large-flowered Himalayan

species, strings and filaments are woven from the anthers a centimetre long, and insects visiting the flowers touch the strings, stick to them, and carry off with them to another flower generally the whole of the contents of the anther in question. The sticky substance is probably a mucilage formed from the outer wall of the pollen-tetrad, or from the broken-down walls of the mother-cells.

Not to be confused with the little pores communicating with the canals containing the oil are the thin portions of the outer layer, into which the intine projects, cæcum-like, as it swells up in water. It often looks as though the extine were actually perforated at these places; this, however, is not the case, and it is not till later, when the intine pushes through and the pollen-tube is formed, that these places are burst and true apertures arise.

The variety exhibited by these spots is as remarkable as that of the sculpturings. The outmost layer often thins out at those spots where the wall is grooved. As the grain swells up in water, the extine often bursts at the thin region, and may actually peel off (*cf.* fig. 217 [10]). In *Mimulus* and *Thunbergia* the thin region has the form of a spiral, or it may run into loops and convolutions, as shown in 217 [9]. When the intine swells up and bursts the extine, the pollen-grain looks as though it had been pared. In the Passion-Flower the thin places are ring-like, so that with the swelling of the intine, the extine comes away in the form of little lids. The same thing happens in the Gourd, where the lids are very small, and are provided each with a little spine (fig. 217 [3]). A curious condition obtains in *Morina Persica* (allied to the Teasel, *cf.* fig. 217 [2]). Each of the pollen-grains has at its equator three projections, resembling closed bottle-necks with swollen, circular mouths. Very frequently the thin places are disc-like, and may be compared to the glazed port-holes of a ship. It is especially this form which suggests that the outmost layer of the wall is perforated from the beginning. In Umbelliferæ, Rosaceæ, Papilionaceæ, Violets, Rutaceæ, Hypericineæ, Scrophulariaceæ, and other groups of plants, the little circular windows lie hidden in the grooves; in *Cobæa scandens* (217 [1]) they are in the "cells" of the honey-comb, and in Onagraceæ, *e.g.* Enchanter's Nightshade (*Circæa*), the outer coat is continued as a thin investment over the tops of the projecting warts (fig. 217 [5]). The number of windows varies from plant to plant. Cyperaceæ have one; Bromeliaceæ and the Meadow Saffron, Figs and Brugmansias two; Nettles, Oaks, and Beeches, Evening Primroses and Willow-herbs, and many other plants three; Alders and Birches four to six; Currants eight to twelve; Convolvuluses fifteen to eighteen; Carnations, Oraches, and Mezereons twenty to thirty; and Nyctagineæ over thirty.

Having concluded the description of the walls of pollen-grains, the question arises, for what purposes are all these remarkable structures, these grooves and striæ, these chinks and furrows, thorns and spines developed? What is the meaning of the coats of oil and viscin? What of the thin places, and windows, and tiny lids?

Of these the last question is the easiest to answer. As observation shows, pollen-grains swell up with lightning rapidity when they are placed in water. The

protoplasm within, destined for fertilization, takes up water from the environment very quickly and energetically. In consequence it swells rapidly, and must have an inclosing wall which will not impede its rapid stretching. For this purpose the thin places and folds are admirably suited. Through them fluids readily pass to the interior, and simultaneously the grooves (previously folded inwards) become inflated, and the pollen-grains come to occupy two to four times the space they previously did. The thicker portions, saturated with oil, play a purely passive rôle in these events. Water cannot enter by these parts, nor do they stretch with the swelling up inside. Later, when the intine has grown out and assumed the form of a tube, the outer wall is not essentially altered. The thin spots have been ruptured, and where lids are present, they are raised; the protoplast, enveloped in the tube-like intine, vacates the extine by one of the thin spots, much as a germinating embryo does its seed-coat. Just as it is of advantage in germination for the seed-coat to be fixed on the substratum, whilst the young plant gets a good hold of the ground, so here it is of value to the young pollen-tube as it quits the extine of the pollen-grain that the coat should be fixed firmly; for this purpose the various ridges, teeth, and spines possess a high significance, serving as a means of anchoring the pollen-grain whilst the pollen-tube is being formed.

But the most important service rendered by the sculpturings and inequalities of the walls consists in the fact that thereby considerable quantities of pollen-grains are enabled to cohere in crumbling masses to the slits of the opened anthers, and to become attached to insects and other animals visiting the flowers for food. Contrasting with this *clinging pollen* is the already-mentioned *dusty pollen*, with smooth and non-adhesive surface. Dusty pollen does not cohere in clusters, nor does it readily attach itself to foreign bodies. On the other hand, the least disturbance or breath of air carries it away in clouds.

It is sufficiently obvious that globular or ellipsoidal pollen-grains with smooth surfaces will be distributed in the form of dust more readily than grains possessing an angular or crystalline form. The former have a smaller surface of contact than the latter. When the surface is, in addition, variously sculptured and raised into folds and inequalities, the points of contact are of course enormously increased. The little projections of the surfaces of adjacent grains interlock like the wheels of a watch; longer ones become entwined like fingers; thus it comes to pass that hundreds of neighbouring pollen-grains hang together like burs. That such masses will readily attach themselves to the hairs, bristles, probosces, and legs of insects hardly needs further demonstration.

This capacity for clinging is much increased when the surfaces of the grains are saturated with oil. The sticky property of the viscin has been already enlarged upon. We may thus summarize the whole matter in the statement that the crystalline forms, the various sculpturings, spines, and other projections, as well as the presence of oil and viscin on the surface are arrangements in virtue of which the adhesiveness of the pollen-grains is increased.

According as one or other of these arrangements is present or absent we find

every degree of cohesiveness in pollen—dusty, floury, crumbly, clotted, glutinous, waxy. A marked contrast is noticeable between flowers the anthers of which produce dusty, and those which produce coherent pollen. So pronounced is this, that we shall treat of the pollination of these flowers, and in particular of the transmission of the pollen from flower to flower, under separate headings. Here it need only be added that this distinction between dusty and coherent pollen is found not only with isolated pollen-grains but with tetrads. When the stamens of Heaths (*Erica*) are disturbed the pollen escapes in clouds of dust, just as it does from the catkins of the Hazel. This dust, however, consists, not of isolated pollen-cells, but of tetrads. In Azaleas and Rhododendrons, on the other hand, the pollen-tetrads cling together into sticky filaments, just as do the isolated grains of the Evening Primrose and Willow-herb.

Why it is that the pollen is in some cases in tetrads and in others in isolated grains, why its adhesiveness is promoted by such various means as those enumerated, is difficult to say. These differences are perhaps connected with the varying form of the insect-visitors which carry the pollen away, and of the stigmas upon which it is deposited. That the sculpturings protect the pollen against untimely wetting will be shown in the following chapter.

PROTECTION OF POLLEN.

The approach to Venice from the mainland is by a long embankment, on either side of which the traveller commands an endless vista of marshes full of reeds and rushes broken here and there by expanses of brackish water—the famous lagoons—which themselves exhibit a luxuriant vegetation consisting principally of Pond-weeds and Naiadaceæ. One plant in particular, the Grass-wrack (*Zostera*), is conspicuous for its abundance in the lagoons, covering, as it does, extensive tracts of the sandy mud at the bottom of the shallow water. The leaves are submerged, ribbon-shaped, and of a brownish-green colour somewhat resembling sea-weed, and, when collected and dried, they are known in commerce by the name of "Sea-grass", and are used in the packing of glass, and of late years also for stuffing mattresses and cushions. These Grass-wracks, of which there are two known species, differ so greatly from other Phanerogams, not only in appearance, but also in development and in the mode of pollination, that one might almost be induced to assign to them and their immediate allies a special class, were it not that the fact of the existence of numerous intermediate forms and connecting links tells against their isolation.

In the first place, the pollen in *Zostera* does not possess the outer coat which is so characteristic of the cell-membranes of most pollen-cells. Further, from the moment the pollen-cells are set free by the opening of the anthers—an event which occurs under water—they exhibit the form of elongated cylindrical tubes. In the plants most nearly related to the Grass-wracks, namely, the genera *Posidonia* and *Cymodocea*, some species of which grow in brackish and some in salt water, the long hypha-like pollen-cells lie in complicated coils and curves within the anther, and

when they escape from it, and are carried by the water against the long filiform stigmas they adhere to those structures as do the spermatozoids (spermatia) to the trichogyne in the Red Sea-weeds (*cf.* pp. 60, 61). The filamentous pollen of *Halophila* is even divided by transverse septa into several chambers, or, more accurately, the pollen-cells are aggregated into long strings. The pollen-cells are intercepted under water by the filiform stigmas and grow down them into the ovaries. In the different species of *Naias* as also in those of *Zannichellia* the pollen-cells are spherical or ellipsoidal in shape so long as they are inclosed in the anther, but when the anther opens they assume the form of tubes, and are wafted about by the water until they reach the stigmas. The stigma in *Zannichellia* is triangular and comparatively large, and owing to the fact that three or four such stigmas have their edges in contact, a sort of funnel is formed, which serves to collect the pollen-cells as they float about.

The plants above referred to, about fifty species in all, were classed together by the older botanists under the name of *Naiadeæ*, but are now grouped into the families of the Potamogetonaceæ, Naiadaceæ, and Hydrocharidaceæ. They are all aquatic plants, but it would be erroneous to suppose that all the members of these groups possess the same kind of pollen as is exhibited by the Grass-wracks, and the various species of *Halophila*, *Posidonia*, *Cymodocea*, *Naias*, and *Zannichellia*, that is to say, a filamentous pollen destitute of external coat which is conveyed to its destination by currents of water. On the contrary, thousands of aquatic plants discharge their pollen above the surface of the water and not beneath it. The pollen-cells are spherical or ellipsoidal, have a distinct external coat, and are transported to the stigmas not by flowing water but by the wind or by insects. This is the case even in plants whose leafy parts remain under water throughout their lives. *Aldrovandia*, *Hottonia*, and *Utricularia*, many Pond-weeds (*Potamogeton*) and Water-crowfoots (*Ranunculus*), not to mention many others, always raise their flowers above the surface of the water, so that the pollen may escape into the air and be blown or otherwise conveyed from one flower to another. I have observed that even in the case of the various species of Water-starwort (*Callitriche*), which were formerly said to accomplish their fertilization under water, the anthers open only in the air, and that the staminal filaments grow in length according to circumstances until the anthers project above the surface. If they fail to do so, then the anthers of the flowers in question do not open at all; the spherical pollen remains inclosed and decays, together with the anther and its filament, beneath the water. The far-famed *Vallisneria* (see vol. i. p. 667), too, to which we shall return again later on, only emits the pollen from its anthers into the air. The staminiferous buds, it is true, develop under water; but they detach themselves from the axis of the inflorescence in the form of closed bladders, and do not open until they reach the surface. The stamens then project out of the floating flowers into the air, the anthers burst, and the pollen is set free (*cf.* fig. 227). If the buds are kept submerged artificially, neither they nor the anthers open, but they decay, and the pollen perishes under the water. And, as in the case of these aquatic

plants, so also in that of the multitude of plants which germinate and flower on dry land, if the pollen happens to fall into the water or is purposely kept immersed, it is destroyed.

It is thus the fact that the pollen of Phanerogams, with the exception of about fifty species, of which the Grass-wracks may be taken to be the type, is injured by prolonged immersion or subaqueous transport. This obviously suggests an inquiry as to the reason of the hurtful action of water upon cells which require an especial abundance of liquid materials for the development of the pollen-tubes. There is, however, a great difference between the absorption of pure water and the absorption of the liquid substances yielded by stigmas. A pollen-cell deposited upon a stigma gradually takes up the liquids there available, and the pollen-tube pushes out comparatively slowly. If, on the other hand, the pollen-cell is put into water, or is in nature so wetted by rain or dew as to be practically immersed in a water-bath, absorption of water takes place almost instantaneously; the intine is pushed out wherever no resistance is offered by the extine, and in a moment the pollen-cell swells up. Such a process cannot properly be called a development of the pollen-tube. No real growth can take place in so short a time, and what has occurred is simply an expansion of the intine and a smoothing out of the folds which have hitherto lain tucked in. Frequently, indeed, the limits of elasticity are exceeded; the projecting part of the intine bursts, and the spermatoplasm flows out into the water in the form of a finely granulated, slimy mass. In that event the pollen-cell is destroyed, and comes to nothing. But even if the intine does not burst, the pollen undergoes such complete alteration through the rapid absorption of water that its protoplasm loses the power of fertilization. It seems as if the protoplasts inclosed in pollen-cells, subjected to prolonged immersion, were literally drowned. Thus much is certain, that the immense majority of pollen-cells perish under water, and that even if wetted they incur great risk of destruction. This danger, which may be of daily occurrence in case of rain or heavy dew, has to be avoided. In order to preserve the pollen fit for use it must be secured by protective apparatus against the injurious effects of moisture, especially against atmospheric deposits; it must be able to develop under conditions from which this factor—in so far as it is harmful—is, generally speaking, excluded.

In regions where there is a regular alternation of rainy and rainless seasons—in the llanos of Venezuela, the Brazilian campos, the dry districts of India and the Soudan, above all, in the parts of Australia to the south of the tropic where the rainfall is limited to the winter and afterwards ceases for months—the climate itself indirectly affords security to the pollen against risk from water; or, in other words, any apparatus to protect from rain the pollen of plants which flower in rainless seasons would be superfluous. The trees which wave above the grass of the wonderful savannahs of Australia, as also the numerous dry and rigid shrubs which belong to the adjacent "scrub", do not flower until the rainy season is over, when the flowers do not run any risk of being drenched with rain. In the absence of the danger the necessity for any direct means of defence against it also

disappears, and in Australia the numerous Mimoseæ and Myrtaceæ and the Proteaceæ, which constitute the principal part of the dense copses just referred to, are accordingly destitute of any contrivance capable of acting as a protection to the pollen. These plants preserve their rigid character even during the flowering season; the filaments bearing the anthers project in large numbers far beyond the small floral envelopes in the Acacias and in the innumerable species of *Callistemon*, *Melaleuca*, *Eucalyptus*, *Calothamnus*, and *Metrosideros*, and the styliform prolongations of the ovaries in Proteaceæ, on the top of which the pollen is deposited when set free from the anthers, spring up and stretch out unprotected far beyond the restricted perianth.

Flowers which inhabit a region where moisture is deposited from the atmosphere in greatest quantity in the flowering season exhibit an entirely different form. In the mountains of Central and Southern Europe, where this coincidence occurs, the plants whilst in flower must be prepared for daily showers. In addition every plant drips with dew in the early morning, and drops of water are deposited on leaves and flowers in the course of the day by the mists as they roll by. It must often happen that the pollen remains for days together hanging to the opened anthers before it is carried away by bees or butterflies to the stigmas of other flowers. Here if anywhere is an instance of the necessity of ample shelter for the pollen. Examine the plants composing the smaller brushwood of such a region, and you will find how great a contrast they afford to the plants of the thickets of Australia. The flowers of the Heather (*Calluna vulgaris*), and of the Bilberry, Bog Whortleberry, and Cowberry (*Vaccinium Myrtillus*, *V. uliginosum*, *V. Vitis-Idæa*) have bell- or cup-shaped corollas which hang down from curved stalks with the mouths of the flowers towards the earth, and so cover the pollen-laden anthers. Similarly, we find the Alpine Rhododendrons ("Alpine Roses"), which clothe the mountain sides, with flowers inclined at a right angle to the erect stalks so that the anthers are perfectly sheltered beneath their tilted bells.

All the many contrivances whereby pollen is directly protected from wet are of the same nature as the above, the method of protection being by some such roofing in or envelopment of the anthers. That these adaptations should exhibit so much variety in detail in spite of the uniformity of their object is due to the condition that the envelopment must itself not be carried too far. On no account must the dissemination of the pollen or its transport by wind or insects to the stigmas of other flowers be hindered; nay, the very same parts of a flower which shelter the pollen from rain frequently have the additional function of assisting the dispersion of the pollen when the rain is over.

In the enumeration of arrangements for warding off injury to pollen from wetting, the various coverings and protections are described as equally effective for rain as for dew. But this, of course, is not for the same reason. A roof protects structures from rain by intercepting the drops, and from being bedewed since it diminishes radiation from the bodies beneath and thus keeps them at a

gher temperature than would otherwise have been the case. This explanation ust be borne in mind.

We find, therefore, an amount of variety in the forms of safeguard against ret corresponding to the multiplicity of the adaptations which subserve the purpose of pollen-transport by the wind or by butterflies, bees, beetles, or flies, as the case may be. The means of protection are diversified also according to whether the cover is placed immediately over the pollen or over an entire group of flowers, whether it shelters the newly-opened, pollen-laden anthers or that part of the flower whereon pollen liberated from the anthers is temporarily deposited; and again they vary according as it is the anther-walls, stigmas, petals, involucre, or foliage-leaves which have to serve as roof to the pollen. The Lime-tree affords an instance of the last-mentioned arrangement, its flowers being invariably so placed that at the time when pollen is yielded by the anthers they are covered by the broad, flat foliage-leaves. However sharp the showers to which a Lime-tree is subjected the rain-drops roll off the blades of the leaves, and it is only by exception that any one of the many flowers stationed beneath them is wetted. The same provision is met with in a few species of *Daphne* (e.g. *D. Laureola* and *D. Philippi*), in several Malvaceæ (e.g. *Althæa pallida* and *A. rosea*), and in the *Impatiens Nolitangere*, a plant which possesses other remarkable features and will be the subject of further discussion by and by (*cf.* fig. 220[1]). In *Impatiens* the flower-buds are held by their delicate stalks above the surfaces of the leaves from whose axils they spring, and the leaves are at first folded upwards like erect troughs. Subsequently, when the buds get bigger and their stalks longer, the latter slip down to one side of the leaves and hide beneath them, whilst the leaf-margins still continue to be curved upward. The leaf then flattens itself out and fixes the drooping flower-stalk by means of one of the lobes of its heart-shaped base, and thus indirectly keeps the suspended bud in position, so that when later on the bud and its anthers open, which they do simultaneously, they are roofed over by a smooth lamina, off which the rain-drops roll without ever wetting the flowers or their pollen (fig. 220[1]).

In many Aroideæ the spadix is completely covered by the large sheathing leaf or spathe at the time when the anthers burst, as, for instance, in the curious Japanese *Arisema ringens*, where the spathe curves over the inflorescence like a Phrygian cap, and in *Ariopsis peltata*, where the spadix is protected from rain and dew by a sheathing leaf resembling a boat with the keel uppermost (*cf.* fig. 221[1]). *Genetyllis tulipifera*, a shrub belonging to the Myrtaceæ, bears at the ends of slender, woody twigs inflorescences which at first sight might be taken to be pendent tulips. On closer inspection it appears that the large white leaves with red veins which recall the leaves of the tulip perianth are involucral bracts which cover the closely-crowded flowers and shield them from the rain. Similarly in the case of the Banana and its allies (*Musa*, *Ravenala*) the flowers are covered over when the pollen is mature by large involucral sheaths which subsequently, after the pollen has been used up and there is no longer any need

for protection, detach themselves and drop to the ground. Fig. 220[2] shows the male flowers of the dicœcious Sea-Buckthorn (*Hippophae rhamnoides*), which are arranged in spikes and are seated in the axils of scaly bracts at the bases of the young lateral shoots. In each flower are four anthers which discharge their abundant powdery pollen whilst the flower is still closed like a bud and has the appearance of a little bladder (fig. 220[3]). This pollen is of an orange colour, and drops to the bottom of the flower, where it remains (figs. 220[4] and 220[5]) awaiting a dry wind to transport it to the stigmas of the female flowers growing on other plants often at a considerable distance. Several days may go by before

Fig. 220.—Protection of Pollen from Wet.

[1] *Impatiens Noli-tangere.* [2-5] *Hippophae rhamnoides.* [6] *Convallaria majalis.* [7] *Euphrasia officinalis.* [8] *Iris sibirica.* [1], [2], [6], [7], [8] natural size; [3], [4], [5] slightly magnified.

this kind of wind sets in, and meanwhile there is the danger of the store of pollen being soaked by rain or dew and rendered unfit for dispersion. To obviate this risk the pair of curved perianth leaves, which have their concave surfaces turned towards one another, and form, as has been already mentioned, a kind of bladder inclosing the anthers and pollen, dehisce at the sides only. Thus two opposite gaps (figs. 220[4] and 220[5]) are produced, whilst at the top the two valves remain joined together and form an arch completely sheltering the mass of fallen pollen from atmospheric deposits. When the needful wind arises it blows the pollen out through the chinks in the bladder and conveys it to the stigmas of other plants of the same species.

Plants of the Globe-flower (*Trollius*) genus, whose species grow in the Arctic regions in damp situations and also further south in mountainous districts of the

Old World, are daily exposed to rain or heavy dew. Nevertheless their pollen is never wetted, the anthers being completely shut in by the perianth-leaves, which are spirally inserted on the receptacle and closely furled one upon another. These flowers have a ring of stalked nectaries round the stamens, and insects which visit them for the sake of the honey are obliged to break through the roof formed by the overlapping perianth-leaves in order to reach the inside of the flower. The pliability of these leaves enables bees by their weight to effect an entrance, whilst falling drops of rain cannot penetrate, but roll off the flower.

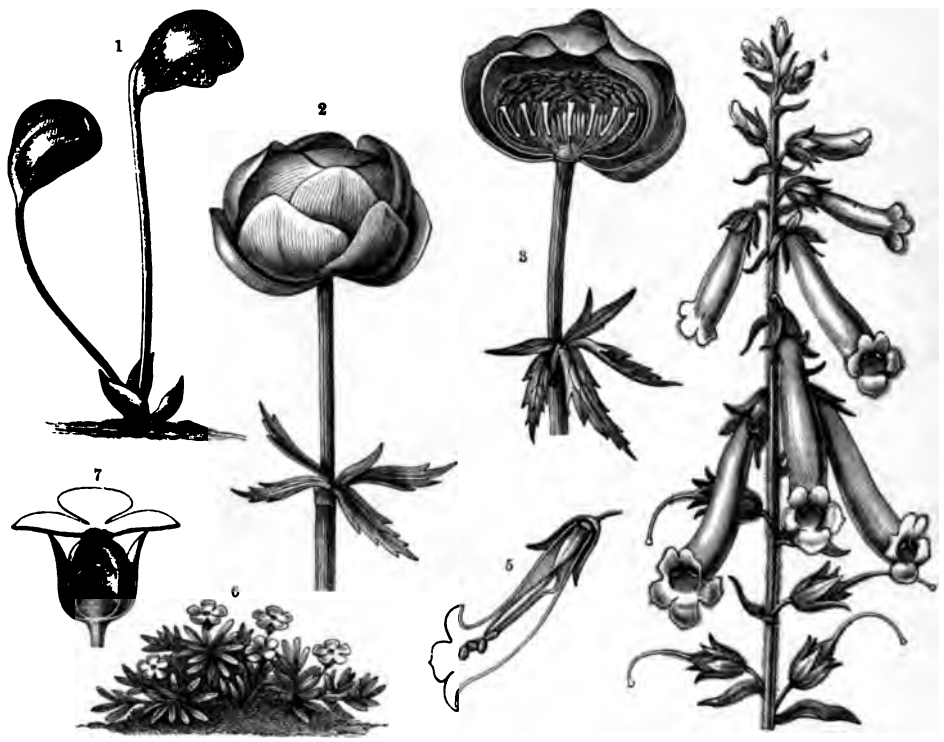

Fig. 221.—Protection of Pollen from Wet.

[1] *Ariopsis peltata.* [2] Flower of *Trollius europæus.* [3] The same with some of the floral-leaves removed. [4] *Digitalis lutescens.* [5] A single flower of *Digitalis lutescens* in longitudinal section. [6] *Arctia glacialis.* [7] Single flower of *Arctia glacialis* in longitudinal section (magnified).

Also in Corydalis, Calceolarias, Toad-Flax and Snap-dragon (*Corydalis, Calceolaria, Linaria, Antirrhinum*) the corolla forms a closed envelope round the anthers; and again in papilionaceous flowers the pollen is, up to the moment of an insect's visit, hidden in the cavity formed by the two petals of the keel.

The majority of lipped flowers—Butterwort, Yellow-rattle, Cow-wheat, and Eye-bright (*Pinguicula, Rhinanthus, Melampyrum, Euphrasia, cf.* fig. 220[7])—as also the Violet (*Viola*), Monkshood (*Aconitum*), and innumerable other plants whose flowers open laterally, do not regularly inclose the pollen, but protect it against rain or dew by means of an arched portion of the flower which forms a roof over it. In *Acanthus* the flowers are inclined laterally, and, though

resembling bi-labiate flowers in general appearance, possess no prominent upper lip, the protection of the pollen being effected by a sepal which stretches out at the place where the upper lip would be. A curious arrangement for the protection of pollen by sepals may be observed in the inflorescence of *Hydrangea quercifolia* (fig. 222[8]), a native of Florida allied to the Hortensias. The flowers of this plant grow in handsome bunches, and are of two kinds: the one kind includes stamens and pistil, but only a very small, greenish, perianth incapable of shielding the pollen of the adjoining stamens from rain or dew; the other has neither stamens nor pistil, but has very large, white, expanded sepals which are arranged so as to constitute with their erect stalks a sort of umbrella. The flowers of the latter type are developed on the outermost and uppermost branches of the inflorescence, and are always in a position to stop the rain from falling upon the umbels of small pollen-bearing flowers which are situated underneath them.

In rare cases the stigmas act as pollen-protectors. The most striking instance is that of the genus *Iris*. The stigmas in the Iris are petaloid, and consist of three foliaceous structures gently curved outwards, and each terminating in a pair of dentate apices (*cf.* fig. 220[8]). The upper surfaces of these foliaceous stigmas are convex and usually somewhat keeled along the middle line, the under surfaces are concave. Beneath each stigma one finds a pollen-laden anther nestling close against the concave surface, and so perfectly concealed that it is impossible that it should ever be reached by a drop of water however heavy the rain.

Flowers of the form called "hypocrateriform" by botanists are adapted to the protection of their pollen on an essentially different principle. The species of *Phlox* and *Daphne* included in this category, the delicate species of Primulaceæ belonging to the genera *Androsace* and *Aretia*, which dwell amid mountain-mists, and the pretty, erect-flowered Primulas (e.g. *Primula farinosa*, *P. denticulata*, *P. Cashmiriana*), all bear flowers which are not roofed in, but have the mouths of their corollas open to the sky, the tubular part of the corolla passing abruptly into an expanded limb (*cf.* figs. 221[6] and 221[7]), so that drops of rain or dew collect on the limb surrounding the mouth of the tube. Here it seems inevitable that some drops of water should reach the anthers inserted in the tube. Yet, as a matter of fact, the pollen is kept dry. For, at the place where the tube passes into the limb of the corolla it is abruptly contracted, besides being often also studded with callosities, in consequence of which the opening is so narrowed that, although insects with fine probosces gain access to suck the honey in the flower, any rain-drops that may happen to be lying upon the limb do not gain admission because the air cannot escape from the tube. If flowers of *Aretia glacialis* (fig. 221[6]), a plant growing on the moraines of glaciers, are examined after a shower, it is found that every one has a drop resting upon it which slightly compresses the air in the narrow tube of the corolla, but cannot reach the pollen upon the anthers lower down the tube. A subsequent shake or puff

of wind causes the drops to roll off the limb of the corolla, or else they are got rid of by evaporation; in either case, the flower becomes once more accessible to insects.

In none of the instances hitherto described does any change take place in the relative positions of the foliage-leaves, petals, or petaloid stigmas, whereby the pollen shall be the better protected. On the other hand, there is a long list of plants wherein the protection of the pollen is effected exclusively by means of changes in the position of some one or other of the leaves in question. This occurs especially in all those species which, like the forms last mentioned,

Fig. 222.—Protection of Pollen from Rain.

[1] Flower of *Eschscholtzia Californica* opened in the sunshine. [2] The same closed in wet weather. [3] Floral capitulum of *Hieracium Pilosella*, closed. [4] Single flower of the same plant. [5] Capitulum of the same, open. [6] Longitudinal section through a closed capitulum of *Catananche cærulea*. [7] Single flower taken from the capitulum in the last stage of flowering. [8] Portion of inflorescence of *Hydrangea quercifolia*. [9] Young closed flower of *Eranthis hiemalis*. [10] Old closed flower of the same.

have the mouths of their flowers exposed to the incidence of rain, or unshielded, so that radiation is not diminished and dew is formed, but, unlike them, exhibit no sufficient constriction of the tubular part of the corolla to prevent drops of water from falling into the flowers. Such unconstricted, cup-shaped, urceolate, infundibular, or tubular flowers would, if upright, constitute regular rain-collectors, and the water would at once saturate the pollen within the flowers. If flowers of the kind close up temporarily and keep their petals or involucral leaves arched over the interior so long as there is any risk of water collecting there, the requisite security from inundation is attained by very simple means. As a matter of fact, protection of pollen is effected in numerous cases by the closing of flowers. Examples of this are afforded by the flowers of Meadow Saffron, Sternbergias, and Crocuses (*Colchicum*, *Sternbergia*, *Crocus*, *cf.* fig. 223),

which lift the cup-shaped limbs of their corollas above the ground in the spring or late autumn, the Gentians of Alpine meadows and their allies of the Centaury genus (*Erythræa*), a host of Bell-flowers with erect blossoms (*Campanula glomerata, C. spicata, C. Trachelium, Specularia Speculum*, &c.), the Peonies, Roses, Flaxes, Opuntias, Mammillarias and Mesembryanthemums, numerous species of the Star of Bethlehem, and Thorn-apple genera (e.g. *Ornithogalum umbellatum, Mandragora vernalis, Datura Stramonium*). The floating flowers of the Water-lily (*Nymphæa*), and the large flowers which are borne

Fig. 223.—Protection of Pollen.

Flowers of *Crocus multifidus*. On the right, flowers open in the sunshine; on the left, flowers closed at night or in wet weather. One of the three closed flowers has some of its perianth-leaves removed.

on the branches of Magnolias also belong to this group of forms. Throughout the day when the sun is shining the floral cups or funnels of these plants are wide open and often even expanded into stars, whilst swarms of insects hover round them; but at dusk when the dew "falls" the petals close up again and overlap one another so as to form a case (*cf.* fig. 223) upon which any amount of dew may be deposited without affecting the interior of the cup. In damp or rainy weather these flowers do not as a rule open. Thus the period of their being closed coincides with a time when most honey-seeking insects are absent, having either gone to rest for the night, or retired to their hiding-places for shelter from the wet.

It is a very interesting phenomenon that petals which close over the anthers

in the evening grow much larger in the course of the flowering period. In many species they become double as long as they were at the moment the flower first opened. The enlargement of the petals takes place *pari passu* with certain processes in the development of the anthers to be protected. Some Ranunculaceæ with erect flowers—*e.g.* the Hepatica (*Anemone Hepatica*) and Winter Aconite (*Eranthis*, *cf.* figs. 222[9] and 222[10])—have their pistils surrounded by a crowd of stamens, and these again encircled by concave perianth leaves (petaloid sepals) which are wide open by day but closed at sunset, forming a dome over the stamens. The anthers of these plants do not open simultaneously, but only by degrees. The pollen on the outermost anthers nearest to the sepals is set free first of all, and this happens at a time when the filaments bearing those anthers are still short. It is obvious that comparatively short sepals suffice to shelter these stamens. Gradually, however, the anthers nearer the middle of the flower open; their filaments elongate, and the sepals would now be no longer of sufficient size to form a dome over all the pollen-laden anthers at night time. They accordingly grow in length day by day, until the anthers next to the carpels yield up their pollen. In the case of *Eranthis* the sepals lengthen in this way from 11 to 22 millimetres (*cf.* figs. 222[9] and 222[10]), and in that of *Anemone Hepatica* from 6 to 13 millimetres; that is to say, they actually double their original length.

A curious instance of the closing of petals is that of *Eschscholtzia Californica* (*cf.* figs. 222[1] and 222[2]). By day the four golden-yellow petals are expanded, the pollen falls from the stamens, which grow in a bunch in the middle of the flower, on to the concave petals, and rests on them in a floury layer as much as 1 millimetre in depth. When evening comes the anthers in the centre, having already lost their pollen, are left unprotected, but each petal furls itself up longitudinally in the prettiest manner conceivable, and thus the fallen pollen is sheltered under four little tents.

The flowers composing the capitula of the Dandelion (*Taraxacum*), Lettuce (*Lactuca*), Chicory (*Cichorium*), Nipple-wort (*Lapsana*), and many other Composites, of which we may here select the Mouse-ear Hawkweed (*Hieracium Pilosella* (fig. 222) as type, have tubular bases, but above are produced unilaterally into a strap-shaped structure to which the term ligule is applied. From the bottom of each ligulate flower spring five stamens whose anthers are connate into a tube. This tube is early filled with pollen discharged introrsely, *i.e.* towards the centre of the flower through longitudinal slits in the anthers. The style is embedded in the tube, and as soon as the pollen is liberated it elongates, and, acting like a chimney-sweep's brush, pushes up the pollen which fills the anther-tube until it rests above the opening at the top. The pollen resting on the top of the style is brushed off by insects when they settle upon the capitula. But it is not certain that insects will make their appearance within a few hours of the extrusion of the pollen, and even if they do they only brush lightly over the flowers, and are sure to leave some of the pollen behind, and this pollen is

then reserved for another destiny which we shall have to consider more carefully later on. In any case the pollen adherent to the projecting end of the style, near the mouth of the tube composed of the connate anthers, must be protected before nightfall, when there will be condensation of dew, or in case of rain being imminent. This protection is, in fact, afforded to each floret by the ligule of the adjoining corolla, which stretches out laterally and constitutes an umbrella. In the Hawkweeds (*Hieracium*) the ligule bends so as to form a covering over the pollen to be protected (*cf.* figs. 222[8] and 222[5]). In *Catananche*, another Composite, each ligule is spread out flat whilst the sun shines, but in the evening becomes concave and at the same time arches over the pollen belonging to its own flower (fig. 222[6]). We cannot here go into all the differences in detail which occur in connection with this form of adaptation. We must not, however, overlook the fact that in these Composites the ligules of the peripheral florets of a capitulum are always much longer than those of the central florets, and that the pollen of the latter shares therefore the protection from wet afforded by the bending over of the outer ligules. We do not mean to say that the short ligules in the middle of the capitulum are not required to take any part at all in sheltering the pollen. In most instances they, too, stand up and curve over inwards, and act in conjunction with the longer outer ones in preventing the entrance of water. The adaptation of the flowers of *Catananche* is carried so far that the long ligules of the peripheral florets cease to bend inwards when there is no longer any pollen to protect in those florets—that is to say, when the pollen has been brushed off and the florets have entered into their last stage of development (*cf.* fig. 222[7]). The short ligulate florets in the central part of the capitulum must then of course see to the protection of their pollen themselves. This is the reason why one sees only the central ligules of old heads of *Catananche* arched inwards, whilst those near the margin remain motionless and stand out in rays during the dewy night just as they do under the noontide sun.

The mechanism for the protection of the pollen is well worthy of notice in those Composites also in which the central florets of the capitula are all tubular and the peripheral florets all ligulate, and in those where the tubular florets are crowded together on a round disc and encompassed by an involucre of stiff leaves which resemble petals. The Marigold (*Calendula*) may be taken as type of the first group, and the Carline Thistle (*Carlina acaulis*) as type of the second (fig. 224). In these plants the style grows and pushes the pollen out at the top of the tubular florets, just as in the case of the ligulate flowers above described it was pushed up through the hollow cylinder formed by the connate anthers, and above each floret a little lump of pollen is seen resting upon the free end of the style. These tubular florets are, however, incapable of securing their pollen against bad weather, and a division of labour is therefore in some degree instituted within the limits of each capitulum, the ligulate florets or radiating marginal bracts, as the case may be, which produce no pollen, being turned to account for the purpose of sheltering the pollen-bearing florets of the centre. In fine

weather the ligulate florets and bracts stand out in rays from the periphery of the capitulum, but in bad weather and at night they are raised and actually bent over the central tubular florets. They are either disposed so as to form together a hollow cone over these florets, or else they overlap one another like the tiles on a roof; often, too, they are twisted together in apparent disorder into a tuft, but they are always so arranged as to afford complete shelter to the central florets and to the pollen exposed by them.

It is a remarkable fact that the length of these incurving rays stands in a definite relation to the diameter of the capitulum. Heads with large discs and great numbers of tubular florets have relatively long marginal rays, those with small discs and few tubular florets have relatively short rays. Moreover, at first when the florets in the middle of the disc are still closed, and only the tubular florets set near the margin have extruded their pollen, the ligulate florets of the ray and the radiating bracts are still short because they only have to shelter their nearest neighbours; but as soon as the flowers in the middle of the disc open, the peripheral florets lengthen so as to be able to cover them also. Thus the roof here actually grows in proportion to the dimensions of the surface requiring shelter.

The changes affecting the position of petals, ligulate florets, and bracts, which have been briefly described and which are classed together under the name of closing movements, take place in most plants in from thirty to fifty minutes, but in a few cases they are much more rapid. Sometimes the process of closing is completed in the course of a few minutes. With Alpine plants it may happen that the flowers shut and open several times within an hour. The warmth imparted by a casual ray of sunshine is sufficient to cause the flowers of *Gentiana nivalis* to spread out their deep-blue petals, but no sooner does the sun disappear behind a cloud than the petals wind themselves round one another in a spiral and close up, forming a hollow cone. If the sun comes out again the corolla is once more open in the course of a few minutes.

In plants with funnel-shaped, tubular, or bowl-shaped corollas, as, for example, the Thorn-apple, Gentians, and the Venus' Looking-Glass (*Datura, Gentiana, Specularia*), the phenomenon of closing is attended by a complex folding, bending, and twisting of the petals; but as a rule the position assumed by the petals on such occasions is the same as that which they previously exhibited in the bud. Generally speaking, most flowers and heads of flowers when closed at night have the same appearance as they had in the bud state.

For the proximate cause of the movements of closing we must undoubtedly look to alterations in the tension of the layers of tissue involved in the operation. These alterations are due chiefly to variations of heat and light. Fluctuations in the degree of moisture of the air may also partly contribute to the result. In the Carline Thistle (*Carlina acaulis*), indeed, the opening and closing of the heads depends solely on this condition, and temperature is only a factor inasmuch as the relative moisture of the air is generally diminished as the heat increases in the parts of the world where the plant grows. Owing to this property of

Carlina acaulis, its large heads of flowers are used as hygrometers and weather-glasses. When the dry bracts surrounding the tubular florets of the capitulum stand out in rays dry weather and a clear sky are indicated, but when the hygroscopic bracts become erect and subsequently converge, so as to form a hollow cone, wet and cloudy weather is anticipated (*cf.* fig. 224). The significance of these movements of the radiating bracts or involucral leaves to the plant itself is as follows. By day when the air is warm and dry the rays have an outward curve and are spread out widely so as to turn their inner surfaces, which are silvery white, to the sky, and they glisten so brightly in the sunlight that they are visible from a great distance. They thus act as a means of alluring insects

Fig. 224.—Protection of Pollen.

Capitula of the Carline Thistle (*Carlina acaulis*), the one on the right open as in the sunshine, that on the left closed as at night or in bad weather.

to the inconspicuous tubular florets of the disc, and these visitors whilst sucking the honey also load themselves with the exposed pollen and subsequently convey it to other flowers. A large number of humble-bees alight on the open capitula of the Carline Thistle, suck the honey from the florets, and at the same time remove the pollen. If at that moment there were to be a sudden shower of rain the florets of the disc would inevitably be wetted and the pollen ruined. But owing to their hygroscopic sensitiveness the rays rear themselves up on occasion of even a slight increase of moisture in the air such as precedes rain, and, bending inwards, unite into a compact tent, off which the drops of rain roll without being able to do any mischief.

Alterations in the form and position of certain tissues of the stamens due to the taking-in and giving-out of water also afford a means of protection for pollen against wet in the case of Plane Trees, and of many Conifers, Yews, and Junipers

in particular. The pollen-cases are in these plants borne on squamous or peltate stalks, which are attached to an axis in a manner similar to the scales of a fir-cone. They also possess in common with the scales of a cone the property of closing and bringing their margins into contact when they are moistened, whereas when quite dry they stand away from one another, leaving wide intervening gaps (*cf.* figs. 226[15] and 226[16] with figs. 226[17] and 226[18]). The pollen-dust which is developed in little spherical pollen-cases on the inner faces of the scales, is very liable to be shaken out of these gaping interspaces, but such an occurrence, as will be presently more fully explained, is only advantageous to the plant if dry weather prevails. In damp weather, and especially during rain, such escape would be equivalent to destruction of the pollen. To avoid this risk the gaps close up, an operation which is effected by the scales absorbing moisture and swelling until their edges are in contact, so that the little pollen-cases attached to their inner surfaces are covered up.

In the flowers hitherto described the parts adapted to the protection of the pollen from wind and wet are all leaf-structures or scaly or peltate outgrowths from the connectives of the stamens, and the adapted structure is bent or hollowed out, expanded or folded, as the case may be. Another group of floral forms, scarcely less considerable than the foregoing in point of numbers, secures this protection in a still simpler manner by bendings of the stalks and stem which convert bowl and cup-shaped flowers into pendulous bells. Usually the inflection occurs shortly before the blossoming of the flower, and then the flower retains the drooping position so long as its pollen is in need of protection. Many Campanulas (e.g. *Campanula barbata, C. persicifolia, C. pusilla*), Solanaceæ and Scrophularineæ (e.g. *Atropa, Brugmansia, Cestrum, Physalis, Scopolia, Digitalis*), Primulaceæ and Boragineæ (e.g. *Cortusa, Lysimachia ciliata, Soldanella, Mertensia, Pulmonaria*), Alpine-roses, Winter-greens and Whortleberries (*Rhododendron, Moneses, Vaccinium*), Ranunculaceæ and Dryadeæ (e.g. *Aquilegia, Clematis integrifolia, Geum rivale*), and many Liliaceous plants (e.g. *Fritillaria, Galanthus, Leucojum, Convallaria*) may be seen with their flower-buds supported on erect stalks and turned to the sky so long as they are closed. But before the flower is quite open the stalk curves downward, and the mouth of the flower is thus directed more or less towards the earth. No sooner has the flowering period expired, and with it the necessity for shielding the anthers concealed in the interior of the flower, than the stalks, in most instances (e.g. *Digitalis, Soldanella, Moneses, Fritillaria, Clematis integrifolia, Geum rivale*), straighten out again, and the fruit developed from the flower—especially if a dry fruit—is once more borne at the end of an erect stalk. The phenomenon is illustrated in figs. 221[4] and 221[5]. It is common to hundreds of plants belonging to most widely different families, and exhibits a great variety of modifications. The limits of this work forbid our discussing all these secondary forms of adaptation, which vary partly according to the structure of the stem and flower-stalks, partly according to the form and disposition of the leaves, petals, and stamens. We can only give a brief account of some of the most striking cases.

If the filaments supporting the anthers charged with pollen are small and short, the perianth, which in the inverted flower constitutes their protective cover, is also of small size, as may be seen, for instance, in the case of the Lily of the Valley (*Convallaria majalis, cf.* fig. 220[6]). A much longer envelope is assigned, on the other hand, to stamens with long filiform filaments. Flowers of the kind possessing large petals but seldom need to be completely pendulous in order to shelter their pollen, it is usually sufficient for them to nod, *i.e.* to droop a little to one side. Thus, for example, the stalks of *Lilium candidum* bend in the flowering season only just enough to incline the mouths of the flowers in a lateral direction. Usually the form of the protective cover is such that the rain can trickle off it in drops. A contrivance far less common is for the petals covering the anthers to form a receptacle out of which the water is periodically emptied. An instance of this is afforded by the South African Sparmannia (*Sparmannia Africana*). The flower-buds are grouped together in umbels, and are borne on stalks, which are curved in a semicircle outwards and downwards away from the main axis, so that the flowers are inverted and their anthers are turned towards the ground and covered over by the petals. When the flower is open, however, the petals are not simply spread out like an umbrella, but are slightly tilted back, *i.e.* upwards. The margins of the petals overlap one another, and their outer surfaces, which, in consequence of the inverted position of the flower are uppermost, thus form a basin open to the sky. When it rains this basin placed above the anthers fills with water, thus adding to the weight borne by the stalk, and as drop after drop increases the strain upon the latter a point is at length reached when the basin tips over, letting the water flow over its edge without wetting the cluster of stamens suspended beneath it. This mechanism preserves the pollen clinging to the dehiscent anthers of *Sparmannia* from rain and dew in spite of their apparent exposure, which to a hasty observer seems to render it inevitable that the stamens should be wetted.

In some plants whose flowers are arranged in racemes a process of inflection takes place before the flowers open, which does not affect the pedicels themselves but the axis from which they spring, the result being that the entire racemes or spikes become pendent. All the flowers are then inverted, and the petals act as a roof in sheltering the pollen adhering to the anthers. This is the case in the Cherry Laurel (*Prunus Laurocerasus*), the Bird Cherry (*Prunus Padus*), the Barberry (*Berberis*), and *Mahonia*. In the Walnut, the Birch, the Hazel, the Alder, and the Poplar (*Juglans, Betula, Corylus, Alnus, Populus*) also, the rachis of the spike changes its position shortly before the dehiscence of the anthers thus providing a shelter for the pollen as it becomes free. The male flowers of these plants whilst in the bud condition are crowded closely together, and form a stiff erect cylindrical spike. But before the flowers open the rachis of the spike grows in length slightly and becomes pendent, whilst the flowers it bears are consequently separated a little from one another and become inverted, so that the floral envelopes, which are composed of little scales and perianth-leaves, are uppermost

and the anthers below them (see fig. vol. i. p. 742). Whilst thus suspended beneath the scales the anthers open and the pollen rolls out. It is not, however, immediately blown away, but falls vertically and collects first of all in trough-like depressions which occur on the external surfaces of the separate flowers. Here it remains until there is dry weather and a puff of wind blows it away to the stigmatic flowers, this being accomplished in a manner that will receive closer consideration later on. Up to this moment its resting-place is sheltered from rain and dew by the flowers situated above it on the same spike, and the appendages of each flower thus constitute, on the one hand, a receptacle for the pollen of the higher flowers, and on the other, a roof over the pollen which has fallen upon the grooved backs of the lower flowers, as is shown in the illustration representing the flowers of the Walnut already referred to.

A special interest attaches to those flowers and inflorescences which assume periodically an inverted position and whose stalks possess the faculty of bending, stretching, or turning concomitantly with the alternations of day and night, and of fine and wet weather. Such plants might quite properly be described as weather-cocks. They include forms belonging to most widely different families, but possessing the common attributes—first, that their flowers or inflorescences are borne on comparatively long stalks, and secondly, that they offer their honey and pollen to the flying insects which visit them in shallow cups or flat saucers, or even on plane discs. In the daytime in fine weather when flowers and inflorescences of this kind straighten out and turn their open surfaces towards the sun, they are plentifully visited by such insects as refuse to enter pendent bells and tubes from underneath, and only alight from above on wide, open, and easily accessible flowers, and thus is effected the important function of pollen-dispersion. On the other hand, by becoming pendent at night and in rainy weather—*i.e.* at a time when insects are not commonly on the wing—they ensure security for their pollen and honey against wet. Hence the periodic movement of the axis appears to achieve a double advantage.

In many Campanulaceæ and Geraniaceæ it is the stalks of individual flowers that bend. The widely-distributed species, *Campanula patula* and *Geranium Robertianum* have been selected from the list of those orders for illustration (*cf.* figs. 225[1] and 225[3] with figs. 225[2] and 225[4]). The same phenomenon occurs in many species of Wood-sorrel, Poppy, Pheasant's Eye, Isopyrum, Crow-foot, Wood Anemone, Cinquefoil, Starwort, Chickweed, Saxifrage, Rock-rose, Anoda, Potato, Pimpernel, Jacob's Ladder, and Tulip (e.g. *Oxalis lasiandra, Papaver alpinum, Adonis vernalis, Isopyrum thalictroides, Ranunculus acris, Anemone nemorosa, Potentilla atrosanguinea, Stellaria graminea, Cerastium chloræfolium, Saxifraga Huetiana, Helianthemum alpestre, Anoda hastata, Solanum tuberosum, Anagallis phœnicea, Polemonium cœruleum, Tulipa sylvestris*). In the Scabious given in the illustration opposite (*Scabiosa lucida*, figs. 225[5] and 225[6]), and in several Composites (*Bellis, Doronicum, Sonchus, Tussilago*, &c.) it is the peduncles bearing the capitula which bend; in many Umbelliferous plants (e.g. *Astrantia*

alpina, *A. carniolica*, &c.), it is the stalks of the umbels, and in some Cruciferous plants (e.g. *Draba aizoides*, *Arabis Turrita*, *Sisymbrium Thalianum*), the axes of the racemes. The above-mentioned Scabious and Composites exhibit a periodic inversion of the entire inflorescence in consequence of the inflection of the axis, and the radiating ligulate florets set round the margin of the capitulum serve to shelter the pollen of the central florets. Similarly in the Umbellifers named, the involucres of the separate umbels, being comparatively large, act in the same way. The fact is also worth notice that in some Willow-herbs (e.g. *Epilobium*

Fig. 225.—Protection of Pollen.

[1] Flowers of the Herb-Robert (*Geranium Robertianum*) in the daytime; the pedicels erect. [2] The same plant with its flowers pendent on curved pedicels, the position assumed during the night and in wet weather. [3] Bell-flower (*Campanula patula*) by day; the flower on erect pedicel. [4] Flower of the same plant inverted for the night or for wet weather, the pedicel being curved. [5] Capitulum of a Scabious (*Scabiosa lucida*) in the daytime; the peduncle erect. [6] Capitulum of the same plant at night or during rain, the peduncle curved and the capitulum inverted.

hirsutum, *E. montanum*, *E. roseum*), the flower-stalks themselves do not bend, but the long stalk-like inferior ovaries curve downward and straighten out again, periodically causing the flowers, which are of a flat salver shape, to alternate between a pendent and an erect position. The inflection of flower-stalks, or, of their substitutes, the ovaries, ceases as soon as the pollen of the flowers concerned has been removed by one means or another, and a shelter for it is no longer needful. The flower-stalks of *Saxifraga Huetiana* only continue to bend so long as the anthers in the flowers they support are covered with pollen, and the long ovaries of the Willow-herbs mentioned above only curve towards the earth on two successive evenings; the third evening,

when there is no longer any pollen to protect from rain and dew, they remain erect.

All these phenomena of inflection and straightening on the part of flowering axes and inferior ovaries are brought about in the same way as the periodic movements of petals and bracts by alterations in the tension of the tissues. These variations of tension are again due partly to vicissitudes in respect of heat and light, and of the degree of moisture of the air. But mechanical stimuli also play an important part, especially such shocks to the flower-bearing axis as are occasioned by the incidence of drops of rain and by gusts of wind. The fact that drops of water are found resting on the nodding or drooping flowers, if the latter are examined before sunrise when there is a heavy dew, or after a shower, tempts one to look upon the inflection merely as a consequence of the strain imposed upon the stalks by the increased weight of the water-laden flowers. No doubt this strain has something to do with the inflection, but it is equally certain that the drooping state does not disappear at once when the water has evaporated and the strain due to its weight has terminated. This persistence of the inflection at all events must be attributed to an alteration in the tension of the tissues of the stem, and no more than the first impulse can be derived from the weight of dew or the impact of drops of rain. Additional evidence of this is afforded by the facts that the process of bending is set up by rain falling on flowers and stem, even when it rolls off immediately, and that pedicels and peduncles also bend over whenever the entire plant is caused to sway about by the wind which precedes a downpour, the stems on these occasions always curving away from the direction of the wind, or, to use a nautical expression, to the lee side.

This phenomenon of the bending of stalks and drooping of flowers before the rain has actually begun looks almost as if the plant had the power of foreboding the approach of bad weather and of adapting itself beforehand in such a manner as to prevent any injury being subsequently inflicted upon it by that destructive agency. Such is the opinion of the peasantry in parts of Europe, and they look upon the inflections above described, as well as the closing of the heads of the Carline Thistle, which was mentioned further back, as a sign of imminent rain. There is, however, as already said, a mechanical explanation of the phenomenon dependent on a change in the tension of the tissues of the stem induced by the oscillations of the plant when subjected to the gusts of wind which usually precede rain, the change of tension being manifested externally by the persistence of the stem's inflection. Moreover, this lasting curvature of the stem may also be produced artificially by inducing the same kind of strain as is caused by the weight of the rain-drops or the vibration caused by rain and wind. If, for instance, you bend the pedicels of various species of *Oxalis* from the erect position they occupy in the middle of the day and hold them down for a time, or if you shake or knock them, the tissues forthwith undergo a change of tension which results in those stalks

becoming curved and the flowers drooping towards the ground instead of facing the sky as before. The same is true of the stalk of a Tulip (*Tulipa*), of the long peduncles of *Doronicum*, of the flower-bearing stems of *Asperula arvensis*, *Astrantia major*, *Cardamine pratensis*, *Lychnis flos-jovis*, and *Primula cortusoides*. If you try to straighten the stalks again afterwards you run a risk of breaking them. An interval of some hours elapses before this inflexibility disappears and the tensions existing before the act of mechanical stimulation are re-established and the stems become straight again.

These different changes in the direction and position of petals, bracts, flower-stalks and stems, which take place concomitantly with the alternations of night and day, of storm and calm, cloud and sunshine, often imply a complete transformation in the aspect of the vegetation within a very brief space of time. On warm summer days, when the sky is clear and the air still, the green of the meadows is sprinkled with the colours of innumerable open flowers. The stellate, salver-shaped, and cup-shaped flowers and inflorescences of Anemones, Ranunculuses, Potentillas, Gentians, and Composites are all wide open, so that the upper brightly-coloured surfaces of their flowers are visible from a great distance. Most of them are turned towards the sun, which enhances their brilliancy; several of the flowers and inflorescences—as, for instance, the Rock-rose (*Helianthemum*)—follow the sun, and face the south-east early in the morning, the south at noon, and the south-west in the afternoon. Countless flies, bees, and butterflies swarm and buzz round the flowers in the sunshine. When the sun sets a cool breeze springs up, and there is a copious deposit of dew on leaves and flowers. The insects withdraw to their homes to rest for the night, and the flowers seem to fall asleep too. Petals fold up, heads of flowers close, flowers and inflorescences bend towards the ground and exhibit the inconspicuous outer surfaces of their floral envelopes to the onlooker. Whilst the night lasts the meadow, drenched in dew, continues in a state of torpor, from which it is awakened once more by the warmth imparted by the sun when it rises next morning. A similar change of aspect occurs when a storm is brewing, when the meadow is swept by wind and rain falls upon the flowering plants. In this event also most flowers cover over or wrap up the parts liable to destruction in time to prevent material damage being done to their pollen.

Comparatively few among ordinary meadow plants appear to be in no way affected by these alterations in external conditions. Some seem to be able to dispense altogether with contrivances for protecting their pollen, for when once the flowers have opened the pollen-cases are left free and uncovered even on occasion of heavy showers. Thus, for example, in *Plantago* and *Globularia* the anthers are borne on long filaments and project in both good and bad weather out of the small flowers, which grow close together in spikes and capitula, and it would seem as though their pollen were exposed to inevitable destruction in case of wet. But closer inspection reveals that even these plants are not destitute of apparatus for the protection of the pollen. To the anthers themselves

is due the security enjoyed by the pollen developed from their tissues. For if dewy nights or wet weather occur after dehiscence has taken place and whilst the pollen is exposed at the apertures in the anther-cavities, the latter close up again and encase the pollen once more. The mature pollen is then protected from wet just as effectually as it was during the period of its maturation, for no injurious effect can be exercised by rain or dew through the walls of the anther upon the pollen-cells concealed within. When there is a return of warm, dry weather the anthers open afresh in the same manner as on the occasion of their first dehiscence. Precisely the same processes as were described on pp. 91–93 are repeated. If the anthers are unilocular with transverse dehiscence, like those of *Globularia* and the Lady's Mantle (*Alchemilla*; see figs. 226 [5, 6, 7, 8, 9, 10]), the sutures open and shut like lips. If the dehiscence is opercular, as in the Bay Laurel (*Laurus nobilis*; see figs. 226 [11, 12, 13, 14]), the valves shut down again and force the pollen adherent to them back into the open recesses of the anthers. Lastly, if the dehiscence is longitudinal and the anther-walls open outwards like folding doors and at the same time become revolute, as in *Thesium* and *Bulbocodium* (*cf.* figs. 226 [1, 2, 3, 4]), the movement is reversed in wet weather, and the two valves close completely together again.

In the Arctic regions and amongst the mountains of Central Europe where copious deposits of moisture occur during the flowering season common to most plants, the number of species possessing anthers which open and shut periodically is not great. Besides those already named, i.e. *Bulbocodium*, *Thesium*, and the *Alchemilla*, only the Plantains (*Plantago*) and Ranunculaceæ, especially those with pendulous anthers (*Thalictrum*), remain to be mentioned as exhibiting this phenomenon particularly clearly. It appears to be much commoner in warmer parts, especially in sub-tropical and tropical regions; at all events, this periodic opening and closing of the anthers is exhibited to perfection in the following plants:—Cinnamon-trees, the Camphor-tree, the Laurel and Lauraceous plants generally, Araliaceæ and Cycadeæ, the various species of *Ricinus* and *Euphorbia*, *Cistus*, the Vine (*Vitis*), and indeed the majority of Ampelideæ, the Tulip-tree and Magnolias (*Liriodendron*, *Magnolia*), and lastly, amongst Conifers the genus *Cephalotaxus*.

The phenomenon in question is the result of changes in the condition of the air in respect of moisture, and depends upon the contraction and expansion of the hygroscopic cells which we noticed in the last chapter as being developed underneath the epidermis of the anther-walls. As in the case of the movements of the involucral bracts on the capitula of the Carline Thistle, the process is only affected by heat inasmuch as the relative degree of moisture in the air alters with a rise or fall of temperature. Seeing that under ordinary conditions variations of temperature and increase or decrease of humidity are connected with the alternation of day and night, it is clear that a periodicity will also be manifest in the opening and closing of anthers, and that in the evening when the degree

of moisture is increased the anthers will close, remain shut throughout the night, and not begin to open again till after sunrise, when the degree of moisture is diminishing.

In cases where both the anthers and the petals of a flower open and close periodically, the corresponding movements are for the most part accomplished simultaneously; but if the cause of the movement is different for petals and anthers it may happen that there is no such unison. For instance, after prolonged rain, the petals of *Bulbocodium* may open under the influence of a

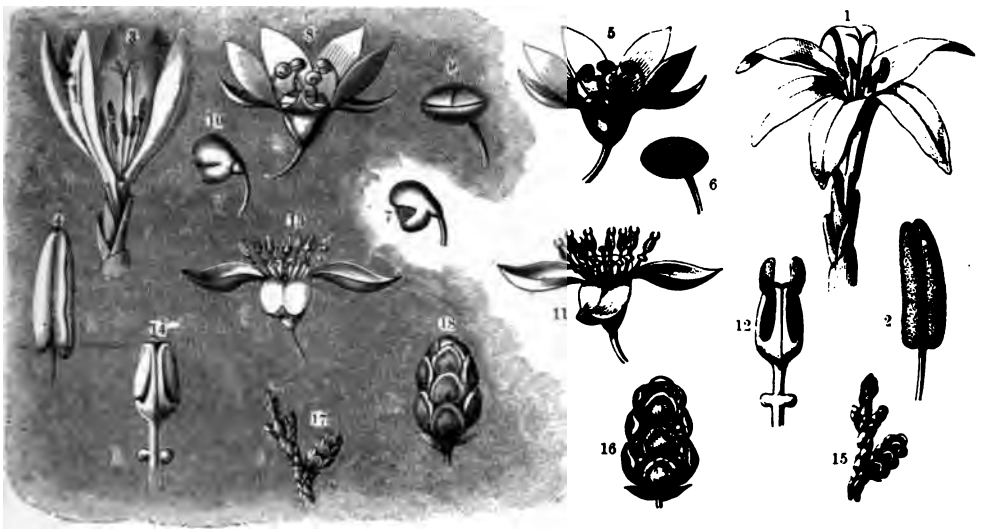

Fig. 226.—Protection of Pollen.

[1] Flower of the *Bulbocodium* with the perianth and the anthers open as they are when the sun is shining and the air dry. [2] An anther from the same. [3] Flower of *Bulbocodium* in moist air; the perianth half open, the anthers closed. [4] An anther from the same. [5] Flower of the Lady's Mantle (*Alchemilla*) with its anthers open in a dry atmosphere. [6, 7] Anthers from the same. [8] Flower of the Lady's Mantle with its anthers closed in rainy weather. [9, 10] Anthers from the same. [11] Flower of the Bay Laurel (*Laurus*) with its anthers open in a dry atmosphere. [12] An anther from the same. [13] Flower of the Bay Laurel with its anthers closed in wet weather. [14] An anther from the same. [15] Staminiferous flowers of *Juniperus Virginiana* in a dry atmosphere. [16] The same magnified. [17] Staminiferous flowers of *Juniperus Virginiana* in wet weather. [18] The same magnified. 1, 3, 15, 17 natural size. The rest × 2 to 8 times.

warm spell of sunshine, whilst the anthers still remain closed owing to the excessive moisture of the atmosphere.

Anthers close up much more quickly than petals on the approach of danger. They usually take only a few minutes, and in many cases not more than half a minute. The anthers of the Bastard Toad-flax (*Thesium alpinum*) shut up within thirty seconds of their being moistened. In this plant the process of closing is rendered additionally interesting by the fact that the moistening of the anther-walls is effected by peculiar tufts of hairs projecting from the perianth. The briefest possible description of this phenomenon will be given here. The open flower of *Thesium* has the limb of its perianth turned to the sky. This position is maintained unchanged day and night, and even the occurrence of bad weather does not cause any alteration in the direction of the flower-stalks or the position of the flowers. Hence rain-drops falling from above and the dew formed on

clear nights must inevitably rest on the open flowers. The immediate wetting of the entire flower is, however, prevented by peculiarities in the form of the limb. The anthers close with great celerity upon the deposition of the drops, the explanation being that the perianth-lobes are connected with the anthers standing in front of them by a bunch of twisted hairs which not only are themselves peculiarly susceptible of being wetted, but conduct the water to the anthers and so cause the anther-walls to close.

A characteristic manner of protecting the pollen by means of the anther-walls after the pollen has been set free, and when it is ready to be carried away by insects, may be observed in several Composites (e.g. *Onopordon*, *Centaurea*). There is no material difference between these plants and the other Composites discussed on p. 114 in respect of the structure of the tube of syngenesious anthers, the discharge of the pollen into that tube, or the structure of the style and its situation inside the anther-tube; but an essential distinction exists in the fact that the pollen is conveyed to the mouth of the tube not through the elongation of the style but the contraction of the filiform supports of the anther-cylinder. These filaments in *Onopordon* and *Centaurea* contract in response to mechanical stimuli, and in shortening they pull down the anther-tube with them. The top of the style thereupon becomes visible, for the style is sheathed in the tube, and does not shorten when the filaments do so nor change its position. The pollen resting on the style is consequently exposed, and appears in the form of a pulverulent mass on the top of the style surmounting the anthers. If the mechanical stimulation of the filaments is due to the hovering of an insect about the capitulum, the pollen is no sooner exposed than it is brushed off by the insect, and the entire contrivance is obviously so devised that the same insects as cause (by the touch of their legs or probosces) the contraction of the filaments, the retraction of the anther-tube, and the exposure of the pollen may be themselves loaded with the pollen. Up to the moment of the insect's visit, however, the pollen is hidden in the sheath formed by the anthers, and this position is of advantage to it inasmuch as it is there sheltered from rain and dew. The Composites in question have their capitula erect. The capitula of *Onopordon* include neither movable ligulate ray-florets nor radiating bracts capable of closing. *Centaurea* has trumpet-shaped marginal florets, but they do not possess the power of arching over and protecting the tubular florets of the centre. The stalks of the capitula become neither pendent nor nodding in wet weather. In short, the pollen of these particular Composites is destitute of any of the various means of protection which are present in other genera of the same family and which have just been discussed. But instead, the anther-tube itself undertakes the task of sheltering the pollen after the latter is liberated until the moment when the insects which are to carry it away alight upon the flowers.

We need only notice incidentally that extrorse anthers, which turn their recesses filled with coherent masses of pollen towards the earth and their backs to the sky are also to a certain extent protected against wet. A more impor-

tant provision at all events consists in the fact that the injurious effect of rain or dew on the pollen-cells may be obviated by certain special sculpturings on the surfaces of these cells. Reference has already been made to such cases at the conclusion of the last chapter. They are on the whole rare, and are limited apparently to plants of the tropical and sub-tropical regions. The pollen of the beautiful climbing *Cobœa scandens* (*cf.* fig. 217 [1]), one of the Polemoniaceæ, will serve as an example. On the surface of this pollen may be observed a number of little pits with angular rims which make it look at first sight almost like a honey-comb. The pits are not, it is true, so deep as those of a honey-comb, but they are deep enough to prevent the air with which they are filled from being displaced by water dropping upon the pollen. Thus air remains in the pits and thereby affords protection from wet, for it forms an intermediate layer separating the thin parts of the cell-membrane from the water. The thick layers of the cell-membrane which project in ridges are still liable to be wetted, but water cannot penetrate at once through them into the interior of the cell, and such an entrance it is that constitutes the greatest danger to the pollen. A gradual absorption of watery liquid—especially that which is derived from the cells of the stigma—is not only not avoided, but is even necessary for the subsequent development of the pollen-cells.

The instances chosen hitherto for the exemplification of the numerous contrivances whereby the pollen in flowers is protected against wet belong, for the most part, to the category of those which have developed one form of protective apparatus only. Frequently, however, two or even three methods of defence co-exist, so that in case one contrivance should fail there is another in reserve. This occurs in cases where the plant has only a meagre stock of pollen, where the number of flowers on one individual and the quantity of pollen-cells produced from each flower are small, and therefore there is not much pollen to waste, where the time allotted to a plant in which to unfold all its flowers is extremely limited, and where the transport of the pollen from flower to flower is accomplished exclusively by flying insects, whose visits are sometimes delayed for several days when the weather is unfavourable. To mention a few instances with more than one means of protection, in many Anemones and Crow-foots, the Hepatica, the Rock-rose, and the Wood-sorrel (*Anemone*, *Ranunculus*, *Hepatica*, *Helianthemum*, *Oxalis*), not only do the petals close over the pollen-laden anthers, but the flower-stalks also bend, causing the flowers to nod. In the Daisy (*Bellis*), the Corn Sow-thistle (*Sonchus arvensis*) and many other Composites not only do the ligulate florets of the ray incline towards one another and form a roof over the pollen of the central florets in cloudy weather and in the evening, but in addition the peduncles become bent or pendent. In *Podophyllum peltatum* the pollen is sheltered by the bell-shaped flower, but in addition to this the peltate foliage-leaves are also spread out over the flowers and act as umbrellas. The synchronous closing of both anthers and petals over the pollen when rain threatens is a phenomenon that may be easily observed in a number of plants, as, for instance, in *Bulbocodium* (*cf.* figs. 226 [1, 2, 3, 4]).

The fact is also worthy of note that identical means of protection have not always been evolved by members of the same family of plants. One has one method of defence, another another. This diversity is exhibited particularly by the various genera of Solanaceæ, and by the multifarious species of the genus *Campanula*. In the Solanaceæ we find the following variety of contrivances according to the genus. The flowers of the Potato (*Solanum tuberosum*) fold up in the afternoon and assume an inverted position owing to the curvature of their stalks for the night, but only maintain it whilst the night lasts. The next morning the flower-stalks straighten, and the flowers unfold again. The Deadly Night-shade (*Atropa Belladonna*) has its flowers inverted during the whole of the flowering season, and it is therefore not necessary for the corollas to open and shut. The flowers of the Mandrake (*Mandragora vernalis*) remain erect, but in the night and in rainy weather the tips of the upright corolla-lobes close over the pollen-covered anthers inside. As regards the different Bell-flowers (*Campanula*), those which have very long peduncles—e.g. *Campanula carpathica* and *Campanula patula* (*cf.* figs. 225[3] and 225[4])—are only pendent in the night and in bad weather; by day and in fine weather they are erect. They exhibit pronounced periodic movements resulting in the curvature of their axes. In other Bell-flowers with shorter stalks—e.g. *Campanula persicifolia, C. pusilla, C. rotundifolia*—the buds nod before they open and continue in this position throughout the time of flowering, whilst in those species wherein the flowers are crowded together in heads and have very short stalks—e.g. *Campanula Cervicaria, C. glomerata, C. spicata*—there is in general no curvature of the axes, but the flowers remain upright and guard themselves against rain by means of an inflection of the points of the corolla towards one another which closes the mouth of the bell. Lastly, in the Venus' Looking-Glass, a plant nearly related to the Bell-flowers, the flower closes by means of deep folds formed in the corolla.

When contrivances have to be described which subserve several purposes at the same time, it would lead to confusion to attempt to say everything that there is to be said about them in one place. In such cases it is much more to the purpose to keep one object alone in view even at the risk of appearing one-sided to a hasty reader. This remark is particularly applicable to the means of protection just described as being adopted by plants to preserve their pollen from wet; for there is no question but that most of these contrivances are capable of rendering other services to the plants in question besides the one specified. In many cases the closing of petals effects not only the protection of the pollen, but also its transference to neighbouring stigmas in the event of a dearth of insect-visitors, as will be explained in a subsequent chapter. If a flower-cup filled at the bottom with honey remained open to the rain the honey would be immediately spoilt and would no longer act as an allurement to insects. Hence we may infer that the shutting of the entrance to the interior of the flower, the construction of the corolla-tube, and the change to a nodding position in the case of melliferous flowers preserve not only the

pollen, but also the honey from being spoilt by the wet. The narrowing of the corolla-tube and the barricading or complete closing of the entrance to the flower also serve, on the other hand, to keep out certain honey-seeking creatures whose visits would not be advantageous to the plant. Finally, these same contrivances may ward off also such insects as would remove the pollen without conveying the least particle of it to other flowers. In connection with this last function there exist, no doubt, special adaptations besides, one of the most striking of which occurs in the Monkey Flower (*Mimulus*) and in the Hemp-Nettle (*Galeopsis*), and is shown in the illustration of a stamen of *Galeopsis angustifolia* (fig. 216 [19], p. 91). In this instance the anthers are furnished with two lids which can only be opened by a certain proportion of the insects visiting the flowers. Insects with bodies of such a size that when they enter the flower they rub the pollen from the anthers on to their backs are able to lift the lids of the anthers by brushing against them, and they thus expose the pollen. On the other hand, smaller animals which would not load their backs with pollen on visiting the flowers in question or would not convey it to the stigmas of other flowers are not strong enough to open the anthers. Thus the pollen is effectively protected by means of these lids against the detrimental action of small-sized plunderers.

DISPERSION OF POLLEN BY THE WIND.

At the beginning of the last chapter it was stated that the medium wherein the transport of the pollen to the stigmas takes place is, in the great majority of Phanerogams, the air. For the conveyance of pollen between flowers situated at a distance from one another there exist two main agents, viz. the wind and insects. Hence Phanerogams have been distinguished by botanists into "anemophilous" or wind-fertilized, and "entomophilous" or insect-fertilized plants. But these terms, which are adopted in most works on Botany, can only be used in a strictly limited sense. It is no doubt true that there are plants in which the transference of the pollen to the stigmas is effected exclusively by the wind, and others in which the equivalent process takes place solely through the intervention of animals; but, on the other hand, it has been ascertained in the case of a large number of plants that whereas shortly after the flowers open small creatures carry off the pollen and convey it to other flowers, later on, when the flowering period is drawing to a close, the pollen is committed to the wind and by it transferred to the stigmas of neighbouring blossoms. The best instances of this are afforded by several of the Rhinanthaceæ, as, for example, *Bartsia* and the Toothwort (*Lathræa*), and by many Ericaceæ, such as *Calluna vulgaris* and *Erica carnea*, but many more could be mentioned. The conformation of the various parts of these flowers when they first open renders a dispersal of the pollen by the wind impossible; but in fine weather insects visit them in large numbers, and in the act of sucking the honey load themselves with pollen

which they afterwards convey to the stigmas of other flowers. Subsequently, however, the conditions are reversed, the supply of honey is exhausted and insects stay away; but, on the other hand, the filaments bearing the anthers have elongated, the pollen-sacs are consequently exserted above the mouth of the corolla, the pollen contained in them is laid bare, and, at the proper time, is blown away by the wind to the stigmas of younger blossoms. Plants of the kind thus appear to have a second contrivance in readiness in case the first fails, so that in any circumstances the object of flowering may be attained. This is indeed a matter of urgent necessity. How easily may it happen that insects are kept away for a long time by unfavourable weather or that they pay but a few visits. Most plants, therefore, take the precaution to provide that under such circumstances the expenditure of energy involved in the production of flowers shall not have been in vain.

It would be inconsistent with the plan of this book to discuss here all the remarkable adaptations which have been evolved for the purpose of providing a supplementary means of dusting the stigmas with pollen in the event of an absence of insects, but it is necessary to make preliminary mention of this one arrangement whereby many flowers, originally entomophilous, subsequently become anemophilous, because it enables us to determine the proper degree of significance to be attached to the division of plants into anemophilous and entomophilous species.

As would naturally be expected, it is, speaking generally, only pollen which is of dusty or floury consistency that is transported by the wind. If it is true, as gardeners assert, that the pollen of Azaleas, which oozes from the anthers in the form of sticky fringes, has on occasion been torn away and conveyed to the stigmas of neighbouring flowers by the wind, the occurrence can only be looked upon as accidental. In ninety-nine cases out of a hundred the viscid strings, if detached by the wind, would not be conveyed to the stigma of another flower, but would adhere to the outside of the calyx and petals, or to the leaves and stem, and would there perish. The same remark applies also to pollen-cells which are bound together into little lumps by oil and viscid substances, or by acicular processes on the outer layer of the cell-membranes. Only in the rarest instances are they carried by the wind to the stigmas of flowers in the vicinity. These are primarily adapted to becoming attached to the bodies of winged insects.

All the more remarkable, therefore, is the fact that in certain water-plants the pollen, though cohering in sticky masses, is blown by the wind on a kind of little boat to the stigmas which are raised above the surface of the water. The phenomenon was first observed in the case of *Vallisneria spiralis*, an aquatic plant which grows in still water, and is widely distributed in Southern Europe. It is, for example, very luxuriant in the ponds, canals, and shallow inlets along the shores of the Lake of Garda, and we will select it as an illustration in the account which follows. The reader is requested first of all to look at the figure on p. 667 of vol. i. It represents a plant living under water with strap-

shaped leaves arranged in fascicles at the ends of the creeping stems which are attached to the mud by root-fibres. In the axils of these leaves a variety of buds are produced—in some cases one only which constitutes the starting-point of a new creeping shoot; in others three close together, one of which grows in length parallel to the bottom and develops a foliage-bud at its extremity, whilst the two others grow straight upward, or there may be two, of which one elongates in a horizontal direction, whilst the axis of the other rises towards the surface of the water. Each of the upward-growing shoots terminates in a kind of bladder composed of two concave and somewhat transparent bracts, one of the pair overlapping the other so as to close the bladder securely. Within these bladders are the flowers. Of the individual plants some develop female flowers only, others male flowers only. The former occur singly in the bladders. Each possesses a long cylindrical inferior ovary crowned by three relatively large stigmas with bi-lobed apices and fringed margins. The stigmas are surrounded by an envelope consisting of an upper whorl of three small abortive petals and a lower whorl of three large ovate-lanceolate sepals. These floral segments are invariably so disposed as to allow the finely-fringed margins of the stigmas to project somewhat beyond the perianth-lobes so that pollen may be caught by the fringes from the side. This is also the reason why the three inner perianth-lobes are stunted, for if they were as large as the outer three the stigma would be covered in at the side and no adhesion of pollen could take place. When the stigmas have reached the stage of being adapted to the reception of pollen, the top of the bladder investing the flower splits; the ovary elongates, flower and stigma are pushed up above the envelope, and appear on the surface of the water, where they are spread out in the medium of the air (see fig. 227). The phenomenon described is only rendered possible by the fact that the stalk of the pistilliferous flower lengthens to an extraordinary extent, and does not cease growing until the flower it bears has reached the surface of the water (*cf.* vol. i. p. 667).

The case of the staminal flowers is utterly different. They are not solitary, but grow in large numbers in a bunch on an axis which stands up in the middle of the investing bladder. The two leaves composing the bladder become disjoined under water, and expose the raceme of spherical buds. The buds are still *in situ* on the rachis, which remains quite short, the inflorescence being held at a height of about 5 centimetres above the mud, as is shown in fig. 155, p. 667, vol. i.

Shortly afterwards one of the most wonderful processes exhibited by the vegetable world is gradually accomplished. The flower-buds hitherto connected with the axis of the raceme by diminutive stalks become detached, ascend in the water, and float about on the surface. At first they are still closed and globular, but soon afterwards they open. The three concave leaflets (sepals) forming the outer whorl of the perianth, which have up to that time been arched like cowls over the stamens, are thrown back and assume the appearance of three boats connected together at one spot, and the stamens, which were originally three in number, but of which only a pair are now furnished with anthers whilst the third

has remained rudimentary, project obliquely up into the air (see fig. 227). The opening of the petals is immediately followed by the dehiscence of the anthers. The coat of the anther shrivels up rapidly, leaving nothing but a little flap upon which the pollen-cells rest. There are generally only 36 pollen-cells contained in each anther. These are comparatively large and very sticky, they cohere together and form a mass of pollen which is borne upon the thick stamen. Notwithstanding the fact that they are very near the surface of the water, the masses of pollen-cells are not easily wetted. The three sepals underneath them form, as has been said, three boats which respond to the slightest movements of the water without upsetting, and therefore protect their freight from wet to

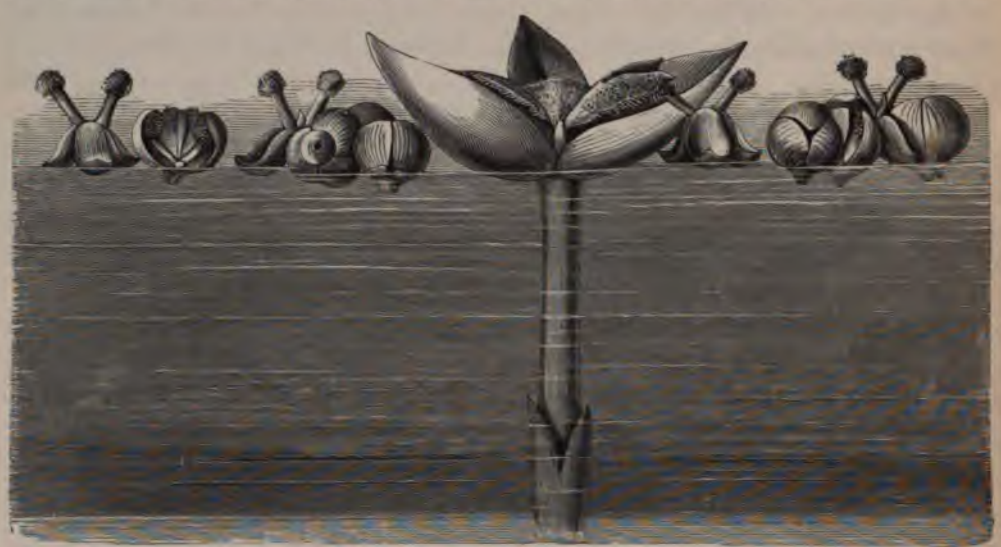

Fig. 227.

Flowers of *Vallisneria spiralis* floating on the surface of water. In the middle a female flower with several male flowers on either side of it in various stages of development; some still closed, some in process of opening, some open with their boat-shaped perianth-lobes thrown back. Projecting from the open flowers are the stamens. An open anther is attaching its pollen to the fringed stigmatic margin of the female flower. ×10.

perfection. These little floats are blown hither and thither by the wind and accumulate in the neighbourhood of fixed bodies, especially in their recesses, where they rest like ships in harbour. When the little craft happen to get stranded in the recesses of a female Vallisneria flower they adhere to the tri-lobed stigma, and some of the pollen-cells are sure to be left sticking to the fringes on the margins of the stigmatic surfaces.

Directly after the adhesion of the pollen, which takes place in the manner shown in fig. 227, the female flower is drawn down under the water. The long flower-stalk assumes a spiral form, and its coils close up so tightly together that the ovary, or young fruit as it now is, is brought to rest at quite a small distance above the muddy bottom of the water.

Up to the present time the conveyance by the wind of adhesive pollen on floats composed of the perianth of the flower is known to exist in the widely-

distributed *Vallisneria spiralis*, in *Vallisneria alternifolia*, which is indigenous in tropical Asia, in *Enalus acoroides*, which grows in the Pacific and Indian Oceans, in *Hydrilla verticillata*, *Elodea Canadensis*, and a few species of the genus *Lagarosiphon*, native at the Cape and in tropical Africa—only 13 species all together, comprised in the little family of Hydrocharidaceæ. This number is almost inappreciable compared with that of the species which produce pollen in the form of fine dust or loose flour, and wherein the pollen is dispersed exclusively and throughout the period of flowering by the wind which blows it away in clouds. It would not be far out to put the number of wind-pollinated plants at 10,000, i.e. at about a tenth of the total number of Phanerogams. To this category belong the Conifers, Oaks, Beeches, Hazels, Birches, Alders, Poplars, Walnut-trees, Mulberry-trees, Planes, and the majority of Palms. All these are of the nature of lofty trees, and usually grow in numbers together, each being associated with others of its own kind so as to form extensive woods or plantations, characterized by a close association of individuals. To these must be added the Grasses produced in meadows, prairies, and savannahs; the Sedges, Reeds, and Rushes characteristic of marshes; the Cereals of our fields; Hemp, Hops, Nettles, and Plantains; the common Pondweeds growing in still or running water, and many other plants belonging to families of the most widely different kinds.

One striking characteristic of these exclusively wind-fertilized plants is the absence of fragrant and bright-coloured flowers. The floral-leaves are comparatively small, of a greenish or yellowish colour, and stand out very little, if at all, from the foliage. The interior of the flower is destitute of honey and perfume. It is of no advantage to these flowers to be visited by insects, and accordingly they have no need of any of the means of alluring bees, butterflies, or flies. Hence the absence of odorous substances, of sweet juices, and of brightly-coloured corollas contrasting with the green foliage and visible from afar. We do not mean to say, however, that the flowers of the plants in question are altogether shunned by insects. Many insects covet the pollen itself, and not infrequently they may be seen hovering about the catkins of Hazels and Birches, on the spikes of Plantains, the panicles of Grasses, Rushes, and Reeds, collecting or devouring the pollen. But these visitors play but a very subordinate part in the dispersion of the pollen. By knocking against parts of a flower that are covered with pollen-dust they may, of course, cause some to fall out, but in so doing they only render a service to the plant if the right wind happens to be blowing at the moment and conveys the pollen to the stigmas. If there is no wind, or it blows in a wrong direction, the plants are more likely to be injured than aided by the insects' visits; for, as the stigmas are not brushed by the pollen-seeking insects and therefore receive no deposit of pollen from them, and, on the other hand, the pollen that they shake out is not likely to be carried to the corresponding stigmas if the air is still, it usually happens that anemophilous plants of the kind thus suffer a loss of pollen without obtaining any compensating advantage.

As has been above implied, however, it is not every aërial current that is adapted to serve as an agent for transferring pollen to stigmas. The least favourable winds are those which are combined with atmospheric deposits. Besides the fact that the pollen-dust would be washed away from its resting-places by the rain and carried to the ground, it must perish in consequence of the soaking. Storms of wind without rain are also anything but beneficial, for they forcibly whirl away any pollen that they encounter and carry it in one direction only, and, as but a small proportion, if any, of the stigmas requiring to be fertilized lie in the path of the wind, the greater part of the pollen is wasted.

The result aimed at is best achieved when the pollen-dust, after being removed from the spot where it has been produced or deposited, is distributed uniformly over an ever-extending area, becoming, in a manner of speaking, diluted and forming a cloud of gradually increasing dimensions but diminishing density, so that the thousands of loose pollen-cells which have up to that time been crowded together within the province of the flower and contained in a space about the size of a pin's head are scattered over an area many million times as great. A gradual dispersion of the kind is only occasioned by a gentle wind. The light breezes which sweep through valleys shortly after sunrise, ascending air-currents such as one perceives quivering over heated plains at noon, the alternating land and sea breezes of the coast-winds which, in passing over cornfields, set the corn in gentle waving motion, and in woods cause a scarcely audible rustle—such are the most propitious agents of pollination. It is easy to observe how, at the proper season, under the influence of a gentle wind of the kind one little cloud of dust after another detaches itself from the flowers of the plants in question and slowly soars away. Owing to the fact that the motion of aërial currents is undulatory and undergoes at short intervals alternate augmentation and diminution, the first motion of the pollen as it dissipates itself is also in waves; but the little cloud is soon withdrawn from observation as it proceeds on its way, and the only thing we can clearly discern is that pollen, like dust raised on a road, ascends in an oblique direction.

The form and distribution of the stigmas to be covered with dust-pollen are also in harmony with these conditions. Most plants, whose pollen is in the form of dust, and transported entirely by currents of air, have dicœcious or moncœcious flowers, and those which develop hermaphrodite flowers exhibit complete dichogamy, that is to say, the andrœcium and gynœcium ripen at different times, so that when mature pollen is being discharged from the anthers of a flower the stigmas of the same flower are already withered, and therefore no longer in a condition to receive the pollen-cells, or else they are still so immature that they cannot be covered with pollen. Any possibility of the transference of pollen from the anthers to the stigmas situated close to them in the same flower being attended with success is as effectually excluded in dichogamous plants as it is in moncœcious and dicœcious species, and the pollen has to be blown to other flowers in the neighbourhood whose stigmas happen to be in

the receptive stage of development. In all these dichogamous plants the flowers with stigmas in the receptive condition are situated higher than the anthers from which mature pollen is being committed to the wind. If you look at any of the species of Plantain (*Plantago*) a few days after they have begun to flower, you find that only the styles with their stigmas ready to receive the pollen project from the uppermost flowers in each spike, whilst the flowers from which pollen is being shaken by the wind occupy the lower parts of the spike.

Fig. 228.—The common Alder (*Alnus glutinosa*).

Branch with flowers that open before the leaves are unfolded; the male flowers grouped in the form of pendent catkins, and above them the female flowers grouped in the form of little spikes. [2] Leafy branch at the top of which are the rudimentary inflorescences for the following spring.

In these lower flowers the stigmas are already withered, in the upper ones the anthers are still closed. Therefore, in order to reach the receptive stigmas, the pollen must travel upwards. The same conditions are found in most species of Sorrel (*Rumex*), in the Wall-Pellitory (*Parietaria*), in Saltwort (*Salsola*), in Arrow-grass (*Triglochin*), and in Pondweeds (*Potamogeton*), and many other plants with hermaphrodite but perfectly dichogamous flowers (*cf.* figs. 236 and 237).

This phenomenon is still more strikingly exhibited by monœcious plants, *i.e.* where male and female flowers occur on the same individual. In the Oak, the Beech, the Alder, &c., the catkins of mature polliniferous flowers hang down

from the branches in the form of swinging tassels whilst the flowers containing mature stigmas are always above them, whether situated on the same or on adjoining branches (*cf.* fig. 228). In Fir-trees, only the pendent lateral branches of the boughs bear the male inflorescences, which at a distance look almost like red mountain-strawberries, whilst the female inflorescences stand up in the form of little cones on the top of the same boughs like tapers on a Christmas-tree; indeed, many Fir-trees bear the female flowers only on the highest branches close to the summit, and on the lower boughs none but male flowers, and under such circumstances pollen could not possibly reach the stigmas if it were only carried by the wind in a horizontal direction. Even in dicœcious plants (*i.e.* where the male and female flowers are on distinct individuals) this relatively inferior situation of the staminal flowers is often to be observed, the end being attained by the fact that the individuals bearing male flowers grow less high than those bearing female flowers. Thus, for example, in Hemp-fields one may see that the plants discharging pollen never reach the same height as those whose flowers are to receive the pollen. Exceptions to the rule do, it is true, appear to exist in the Bulrush (*Typha*), the Bur-reed (*Sparganium*), and many species of Sedge (*Carex*), which possess moncœcious flowers, inasmuch as in them the male flowers are situated above the female; but in consequence of the non-simultaneous elongation of the axis, it usually comes about that the mature female flowers of a plant whose stem is amongst the older and taller ones rests at a higher level than the male flowers of the individual next to it whose stem is younger and shorter, and it is easy to convince one's self by observation that here also the pollen is not conveyed by the wind in a horizontal direction but obliquely upwards, and is wafted to the stigmas of neighbouring plants.

This must not, of course, be looked upon as implying that when pollen is dispersed by the wind none descends; but it is unquestionably true in the majority of cases that the clouds of pollen which are carried off by moderate winds at first soar upwards and either reach the stigmas awaiting them at a higher level direct in their way, or else, later on, when the air is still and the pollen-cells are scattered over a wider space, they sink slowly down, leaving a deposit on the stigmas, just as when dust is raised in a room it ends by slowly falling again and covering the furniture with a uniform layer.

In some species at the very moment when the anthers burst open the pollen is ejected violently into the air and ascends obliquely in the form of a little cloud of dust. In this country a good example of this phenomenon is afforded by the Nettles. Anyone standing in front of a bed of Stinging Nettles on a bright summer morning, and waiting until the first rays of sunshine fall on the flowers, will be surprised to see small pale-coloured clouds of dust ascending here and there from amidst the dark foliage. At first the clouds are solitary, and are given off at measurable intervals; by degrees they become more frequent, and at times one may see five or six or more arising at the same moment and at no great distance from one another. But gradually the little explosions become less frequent again, and

in another half-hour there is an entire cessation of the phenomenon. On inspection one easily discovers that it depends on the fact that the filaments bearing the anthers are coiled in the bud, and suddenly spring up at the same moment that the dehiscence of the anthers takes place.

The species of the genus *Parietaria* and many tropical Urticaceæ behave in the same manner in this respect as our Nettles. As an instance may be taken *Pilea microphylla* (also known under the name of *Pilea muscosa*), which grows

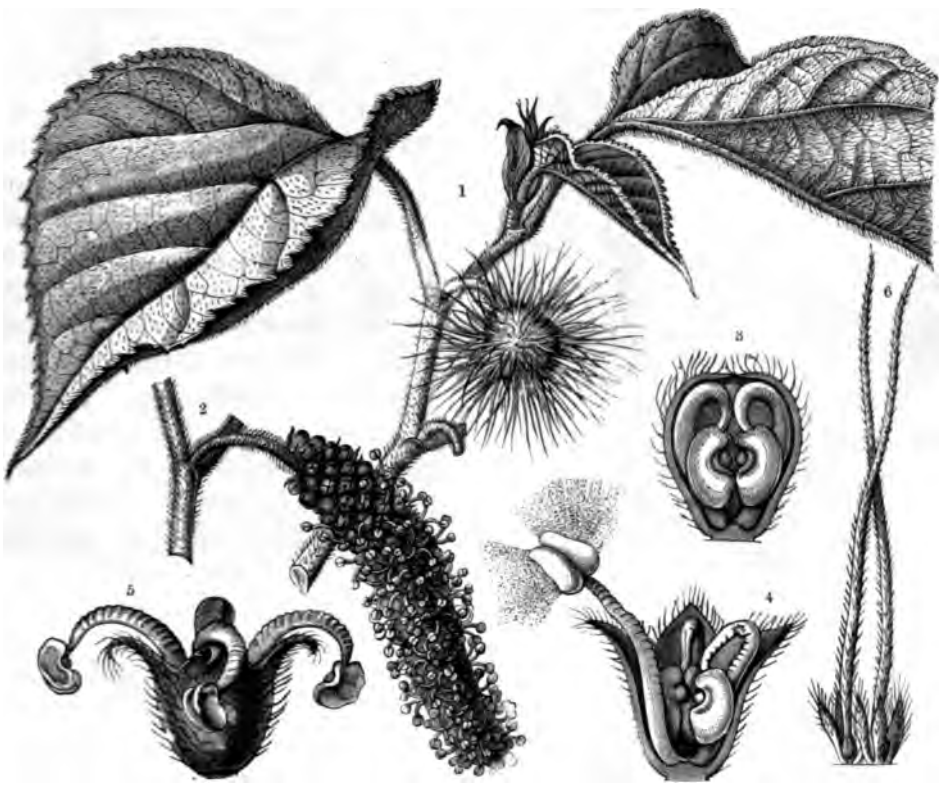

Fig. 229.—The Paper Mulberry-tree (*Broussonetia papyrifera*).

[1] Leafy branch with capitulum of female flowers. [2] Piece of a branch stripped of its foliage with spike of male flowers. [3] An unopened male flower in longitudinal section. [4] An open male flower in longitudinal section; two of the filaments are still tucked in, one has sprung up and is expelling the pollen from the opened anthers. [5] An open male flower with all its stamens already uncoiled and the pollen discharged from the anthers. [6] Two female flowers with long hairy stigmas. [1], [2] natural size; [3–6] ×4–5.

native in Central America, and is often raised in botanic gardens with a view to demonstrating the phenomenon here alluded to. One only has to sprinkle the plant with water at a time when it is covered with flower-buds and then take it out of the shade into the sunshine, and the phenomenon is immediately exhibited. All over the plant the flower-buds explode, and a whitish kind of pollen is discharged into the air in the form of a little cloud. Many Moreæ also display this phenomenon, as, for example, the Paper Mulberry-tree (*Broussonetia papyrifera*), an illustration of whose flowers is given in fig. 229. The male flowers are arranged in spikes (229 [2]), and each flower consists of a sepaloid perianth with four stamens

upon it. The filaments are very thick and, in the closed bud, are tucked in (229 [3]); they are in a state of tension like a spring, but as soon as the cup-shaped perianth opens the filaments spring up one after another, whilst at the same instant the anther-cavities burst open and the pollen is ejected with force into the air (229 [4]). When all the anthers are empty the filaments curve backwards (229 [5]), and soon afterwards the entire spike of flowers drops off the axis, it being no longer of any value to the plant.

In all these plants ejection of the pollen only ensues when a light, dry wind blows at sunrise and causes an alteration in the tension of the tissues concerned. If there is no wind at all, or the air is close and damp, or if it rains, the opening of the flowers and ejection of the pollen do not take place, or rather they are postponed until the atmosphere has become dry again and a breeze arises which causes the flowering branches to sway about. The results of actual observation are of importance to a proper understanding of the dispersal of pollen-dust. For it thus appears that the air in motion has to start two processes which supplement one another, and must operate in rapid succession if the pollen-dust is to reach the right place and not be lost. The same current of air which causes a liberation and expulsion of the pollen by shaking the flowering axes and by altering the tension of the tissues of the flowers, also carries the pollen away from the spot where it has been produced and conveys it to its destined goal; and this statement applies to the full extent not only to the case of resilient stamens, but also to all other instances of anemophilous pollination where the pollen is in the form of dust.

Fig. 230.—The Ash (*Fraxinus excelsior*).

[1] Small bifurcating branch, the left-hand limb of the fork bearing male flowers, the right-hand limb bearing hermaphrodite flowers. [2] Hermaphrodite flower. [3] Two anthers; the upper one open, the lower one still closed. [1] natural size; [2], [3] × 5.

A similar phenomenon is observed in the case of plants with short, thick filaments and comparatively large anthers filled with pollen of a floury consistency. The *Phillyrea*, the Pistachio-nut (*Pistacia*), the Box-tree (*Buxus*), and most Ashes, especially the common Ash (*Fraxinus excelsior*, see fig. 230), may serve to illustrate this group of plants. The development of the carpels in each flower precedes that of the pollen. At a time when the relatively large fleshy stigmas stretch out far beyond the limits of the inconspicuous floral envelope, and are already capable of taking up the pollen, the anthers may be

seen to be still tightly closed (230[1] and 230[2]). The latter do not open till two or three—often even as much as four—days later, and only then in the event of the air being dry. Dehiscence is accomplished by longitudinal fissuring of the anther-lobes. The edges of these fissures contract very speedily, so that each of the pair of anther-lobes is converted into an open recess wherein the pollen lies in the form of a floury or powdery mass (230[3]). Just before dehiscence the

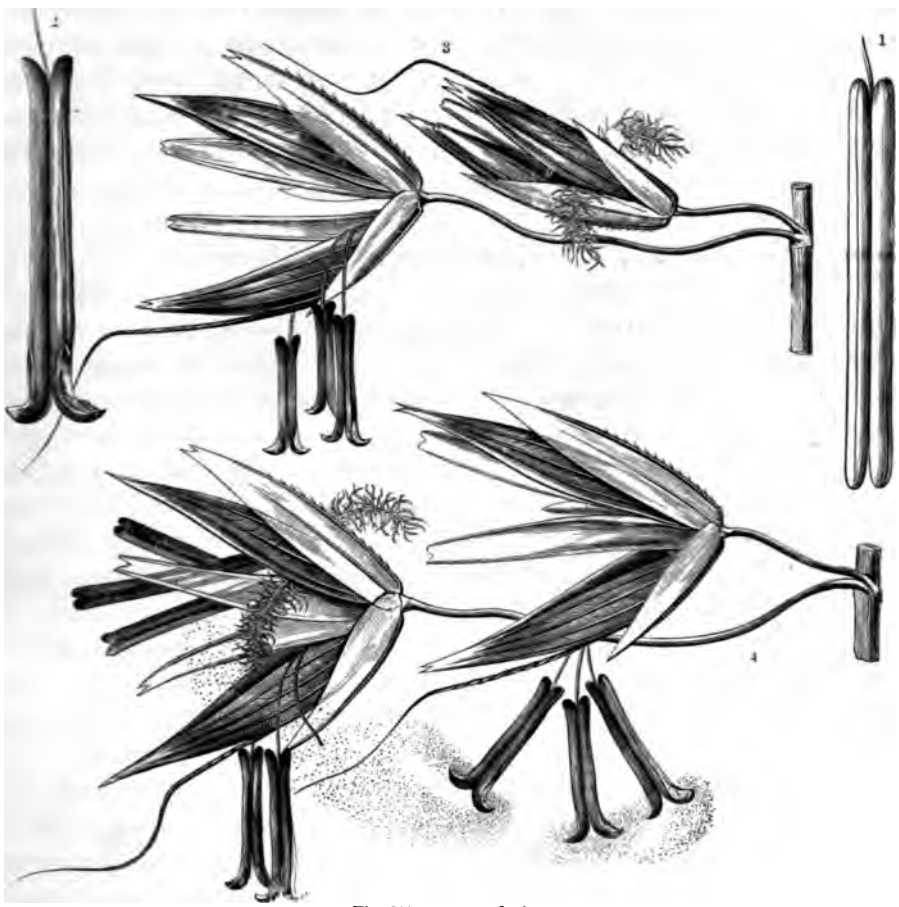

Fig. 231.—*Avena elatior.*

[1] A closed anther. [2] An open anther. [3] Spikelets on a calm day with glumes distended and anthers pendulous. [4] Spikelets in a wind. The pollen escaping from the pendulous anthers in the spikelets to the right; in that to the left (and below) the anthers (two only remaining) have shed their pollen; in a third flower (in the same spikelet as the last-mentioned) the anthers are still closed and in process of being exserted. [1], [2] × 12; [3], [4] × 5.

anthers place themselves in such a position as to ensure the fissure being turned upwards, so that the recesses full of pollen are not emptied so long as the air is still. It is only when the flowering branches begin to sway to and fro that the pollen falls out of the loculi and is blown away in the form of a cloud of dust by the same breeze as set the boughs in motion.

In another group of plants the anthers are borne on long filaments, and are set oscillating and vibrating by the least breath of wind, the pollen being in

upon it. The filaments are very thick and, in the closed bud, are tucked in (229 [3]); they are in a state of tension like a spring, but as soon as the cup-shaped perianth opens the filaments spring up one after another, whilst at the same instant the anther-cavities burst open and the pollen is ejected with force into the air (229 [4]). When all the anthers are empty the filaments curve backwards (229 [5]), and soon afterwards the entire spike of flowers drops off the axis, it being no longer of any value to the plant.

In all these plants ejection of the pollen only ensues when a light, dry wind blows at sunrise and causes an alteration in the tension of the tissues concerned. If there is no wind at all, or the air is close and damp, or if it rains, the opening of the flowers and ejection of the pollen do not take place, or rather they are postponed until the atmosphere has become dry again and a breeze arises which causes the flowering branches to sway about. The results of actual observation are of importance to a proper understanding of the dispersal of pollen-dust. For it thus appears that the air in motion has to start two processes which supplement one another, and must operate in rapid succession if the pollen-dust is to reach the right place and not be lost. The same current of air which causes a liberation and expulsion of the pollen by shaking the flowering axes and by altering the tension of the tissues of the flowers, also carries the pollen away from the spot where it has been produced and conveys it to its destined goal; and this statement applies to the full extent not only to the case of resilient stamens, but also to all other instances of anemophilous pollination where the pollen is in the form of dust.

Fig. 230.—The Ash (*Fraxinus excelsior*).

[1] Small bifurcating branch, the left-hand limb of the fork bearing male flowers, the right-hand limb bearing hermaphrodite flowers. [2] Hermaphrodite flower. [3] Two anthers; the upper one open, the lower one still closed. [1] natural size; [2], [3] × 5.

A similar phenomenon is observed in the case of plants with short, thick filaments and comparatively large anthers filled with pollen of a floury consistency. The *Phillyrea*, the Pistachio-nut (*Pistacia*), the Box-tree (*Buxus*), and most Ashes, especially the common Ash (*Fraxinus excelsior*, see fig. 230), may serve to illustrate this group of plants. The development of the carpels in each flower precedes that of the pollen. At a time when the relatively large fleshy stigmas stretch out far beyond the limits of the inconspicuous floral envelope, and are already capable of taking up the pollen, the anthers may be

seen to be still tightly closed (230[1] and 230[2]). The latter do not open till two or three—often even as much as four—days later, and only then in the event of the air being dry. Dehiscence is accomplished by longitudinal fissuring of the anther-lobes. The edges of these fissures contract very speedily, so that each of the pair of anther-lobes is converted into an open recess wherein the pollen lies in the form of a floury or powdery mass (230[3]). Just before dehiscence the

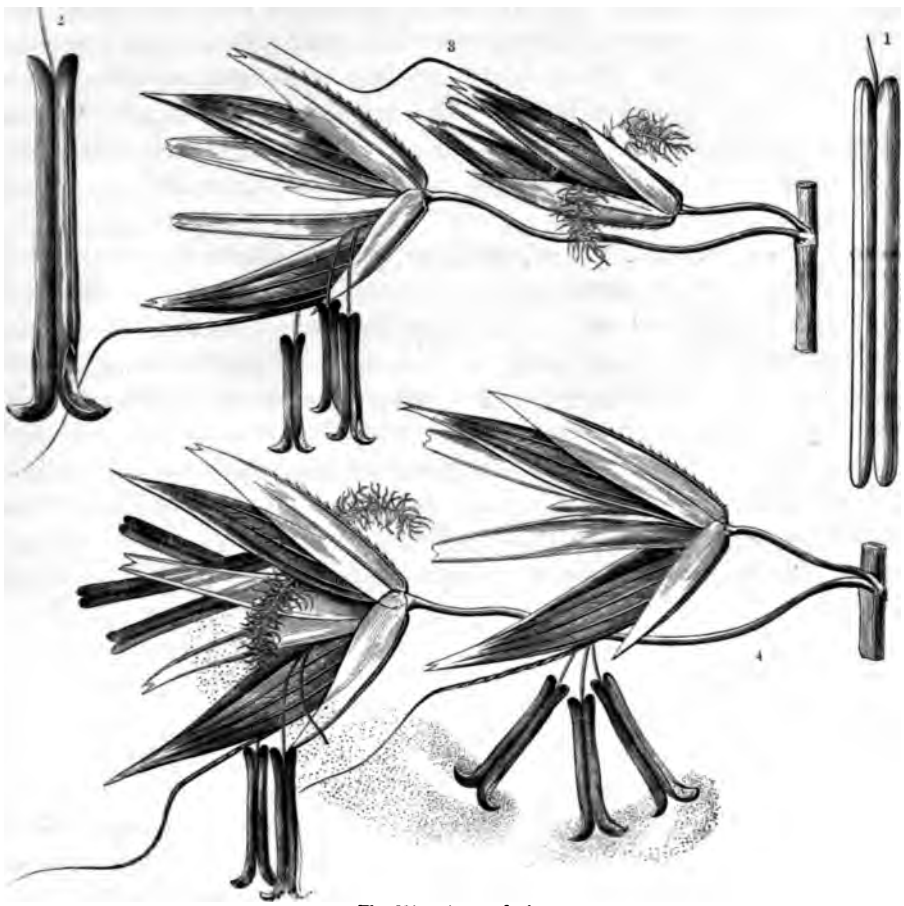

Fig. 231.—*Avena elatior.*

[1] A closed anther. [2] An open anther. [3] Spikelets on a calm day with glumes distended and anthers pendulous. [4] Spikelets in a wind. The pollen escaping from the pendulous anthers in the spikelets to the right; in that to the left (and below) the anthers (two only remaining) have shed their pollen; in a third flower (in the same spikelet as the last-mentioned) the anthers are still closed and in process of being exserted. [1], [2] × 12; [3], [4] × 5.

anthers place themselves in such a position as to ensure the fissure being turned upwards, so that the recesses full of pollen are not emptied so long as the air is still. It is only when the flowering branches begin to sway to and fro that the pollen falls out of the loculi and is blown away in the form of a cloud of dust by the same breeze as set the boughs in motion.

In another group of plants the anthers are borne on long filaments, and are set oscillating and vibrating by the least breath of wind, the pollen being in

consequence discharged in little pinches as though from a sugar-sifter. If the flowers of this kind of plant contain pistils as well as stamens, the relative development of the two sets of organs is always so regulated that the stigmas are already perfect and adapted to the reception of pollen at a time when the anthers of the same flowers are still hidden beneath the floral or involucral envelopes and the pollen is consequently immature. By the time the pollen is completely developed and is in a state to be discharged from the opened anthers, the stigmas of the flower in question are withered and are no longer capable of taking up the pollen. Hence it follows that in these plants the pollen-dust must be transported to other flowers which happen to be at a younger stage of development if fertilization is to be brought about. This is what occurs in nature through the instrumentality of gentle breezes which impose a tremulous motion upon the anthers.

In the first rank of plants belonging to the above category stand the Grasses. Their mode of pollination is so remarkable that it is worth while to look into it a little more closely. One group of Grasses—of which *Avena elatior*, represented in fig. 231, is an excellent example—commences the process under discussion by a sudden distension of the bracts (known by the name of glumes) through the instrumentality of a special turgid tissue situated at their base. The result is that the anthers, till then concealed, are exposed, and it becomes possible for them to be exserted beyond the glumes into the air. This exsertion is effected by an extraordinarily rapid longitudinal growth on the part of the filaments. It has been calculated that in some grasses the filiform filaments elongate to the extent of 1–1·5 mm. in the course of a minute, and that usually in ten minutes they are three or four times as long as they were originally. In one subsection of these plants the filaments grow downwards, in another horizontally, and in a third straight upwards towards the sky. The turgidity of the cells in these delicate filaments is so great as to enable even those which grow vertically upwards to support the weight of the anthers without bending. In the case of those Grasses whose stamens grow downwards from the beginning it does no doubt look as though this direction were assumed in consequence of the weight of the anthers. This is not, however, the fact. A high degree of turgidity exists here also, and if one inverts the inflorescences of this kind of Grass, the stamens which have just completed their longitudinal growth remain quite stiff, in spite of their extreme slenderness, and project straight up. Soon after, it is true, this condition ceases. The filaments become slack; those that were erect nod and droop, those that were horizontal fall down, and the anthers are then all suspended at the ends of oscillating threads.

The dehiscence of the anthers is accomplished synchronously with these changes in the filaments. As long as the anthers lay hidden beneath and protected by the glumes they were straight and linear in form (see fig. 231 [1]). Each anther consists of two contiguous parallel lobes, and each lobe has a line running longitudinally down it, along which dehiscence takes place. This operation

invariably commences after the anther has assumed a pendent position. The filaments and anthers are joined together by a slender connective, and the tissue of this connective is, as it were, articulated so that the anther is capable of turning freely without becoming detached (a condition termed *versatile*). Hence under any circumstances the requisite position can be assumed; that is to say, the at first uppermost ends of the anthers can be made to hang down whether they are on pendent, or on horizontal, or even on erect filaments. When this inversion has been accomplished the anther-lobes open along the sutural lines already referred to. The slits only gape open for a short distance from that extremity of the anther which is now lowest. This partial opening is in some measure dependent on the further circumstance that at the dehiscent portion the two anther-lobes separate from one another and curve round in opposite directions, as is shown in fig. 231[2]. The significance of this inflection lies in the fact that the powdery pollen is prevented from falling out of the loculi the moment the slits are formed. For the curved ends of the anther-lobes assume the shape of little hollow boats in which the pollen may rest for quite a long time if the air is still (fig. 231[3]). It is not till a gust of wind sets the anthers swinging that the pollen-dust is blown away in the form of a small cloud (fig. 231[4], to the right). On the first occasion only the tiny heap pertaining to the dehiscent extremity of the anther is removed, but this is immediately replaced by fresh pollen pouring down from the upper indehiscent portion of the anther. This new supply naturally has no long time to wait, but is blown away by the very next gust. The process may be repeated several times, and generally does not cease until there is no longer any pollen left. When the anthers are quite emptied they drop off the filaments in the form of dry husks. Usually, however, this detachment of the anthers does not take place till several hours after pollination, and in the majority of Grasses, plants which have flowered in the early morning or during the day still have their empty anthers hanging to the spikes or panicles, as the case may be, at sunset.

The changes preceding pollination are much more markedly dependent on the weather in Grasses than in other plants. The temperature and hygroscopic condition of the air in particular play an important part. Rain and low temperatures may delay the splitting asunder of the glumes and the extrusion and dehiscence of the anthers not merely for hours, but for days. A very dry atmosphere accompanied by a high temperature also has the effect of retarding the processes above described. The most favourable conditions for pollination in the case of most Grasses prevail in the early morning at an hour when there is still some dew lying on the meadows, when the first rays of sunshine fall obliquely upon the flowers, and the temperature is rising gently and a light breeze sets the spikes and panicles in motion. Under such external conditions as these the phenomena of flowering and pollination are accomplished with astonishing rapidity. In some Grasses an observer may see the glumes relax and spring open, the stamens grow out, the anthers open and the pollen scat-

tered, all in the space of a few minutes. The earliest discharge of pollen begins between 4 and 5 a.m. in the height of summer, and the plants which take part in it thus early are the Meadow-grass (*Poa*), *Kœleria*, and *Avena elatior*. A little later, between 5 and 6 o'clock, comes the turn of the Quaking-grass (*Briza media*) and *Aira cæspitosa*, and of Wheat and Barley (*Triticum*, *Hordeum*). Between 6 and 7 pollination occurs in Rye and in a great number of different Grasses which grow in meadows, such as Cock's-foot-grass (*Dactylis*), *Andropogon*, the Brome-grasses (*Brachypodium*), and many species of Fescue (*Festuca*). Between 7 and 8 o'clock the pollen is liberated from Oats of the *Trisetum* group, from the Fox-tail-grass (*Alopecurus*), Timothy Grass (*Phleum*), and the Sweet Vernal Grass (*Anthoxanthum*). An interval now intervenes, at least amongst the indigenous Grasses. Of exotic species which are cultivated in gardens the following discharge their pollen in the course of the forenoon, viz. the Millets (*Panicum milliaceum* and *Sorghum*) between 8 and 9 o'clock; *Setaria Italica* and the Brazilian Pampas-grass (*Gynerium argenteum*) between 9 and 10 o'clock. Towards noon indigenous Grasses come again into play. About 11 o'clock pollination takes place in most species of the Bent-grass genus (*Agrostis*), and between 12 and 1 in Melic-grass (*Melica*), *Molinia*, Mat-grass (*Nardus*), *Elymus*, *Sclerochloa*, and several species of *Calamagrostis*. In the course of the afternoon the process takes place in a few isolated species, as, for instance, in some Brome-grasses at 2 o'clock, in a few species of Oat (*Avena*) at 3, in *Agropyrum* at 4, and in *Aira flexuosa* between 5 and 6. It is worthy of note that the Soft-grass (*Holcus*), under favourable atmospheric conditions, opens its glumes, pushes forth its anthers, and liberates pollen twice a day, once in the morning at about 6 o'clock, and a second time in the evening at about 7—provided always that the temperature of the air is not less than 14° C. The entire process lasts in most cases from 15 to 20 minutes for each flower.

With the opening back of the glumes and extrusion of the anthers are often connected alterations also in the position and inclination of the stalks which bear the spikelets. For example, the pedicels of the spikelets of *Agrostis*, *Apera*, *Calamagrostis*, *Kœleria*, and *Trisetum* divaricate from the axis, so as to form with it angles of from 45° to 80° for the period of pollination. But as soon as the pollen is discharged all these stalks move back towards the main axis of the inflorescence, and the panicle, as it were, contracts. These movements are obviously designed to give sufficient room to the anthers when they are exserted, in order that they may oscillate freely and so disperse their pollen. In those Grasses where the flowers are crowded together in close spikes, and also in the large *Carex* section of the Cyperaceæ, the bracts do not spring open but only relax, and sometimes merely to such a slight extent that it is scarcely noticeable on cursory inspection. The thread-like filaments are also only partially visible in cases of the kind, the anthers are pushed forward and raised above the glumes through the rapid growth of their filaments. As soon as a filament reaches the proper length its upper

extremity becomes pendulous, and the anther hangs from it and encounters no obstacle to movements such as are required to shake out the pollen.

As in the case of Grasses and Sedges, so also in Hemp and Hops (*Cannabis*, *Humulus*), and in numerous species of Sorrel and Meadow-rue (*e.g. Rumex alpinus* and *R. scutatus*, *Thalictrum alpinum*, *T. fœtidum*, *T. minus*) the pollen-dust is shaken out of anthers which are pendulous at the ends of delicate filaments; only,

Fig. 232.—The Elm (*Ulmus campestris*).

[1] With flowers. [2] With fruits.

in these plants not glumes but small perianth-leaves form the protective envelope round the anthers before they open. Moreover, in Hemp and Hops, and the above-mentioned species of Meadow-rue, the anther-lobes do not burst wide open when they dehisce, but exhibit parallel slits which are at first so narrow that the pollen can only shake out little by little. Plantains (*Plantago*) also have their pollen shaken out of the anthers, which are borne on long filaments, by the wind. The filaments are tucked in so long as the flower is in bud, but when the petals unfold the filaments straighten out and project beyond the floral spike. The versatile

anthers borne by these filaments are broad and for the most part heart-shaped; the two lobes of which each anther is composed only open on the side turned to the sky,

Fig. 233.—Mountain Pine (*Pinus Pumilio*).

[1] A single polliniferous scale (stamen) seen from above. [2] Three polliniferous scales, one above the other, seen from the side. The pollen falling from each anther alights on the upper surface of the stamen next below. [3] Two spikes of polliniferous scales. [4] Branch with apical group of staminal flowers from which pollen is being discharged. [5] Female flower. [1,2] ×10; [3] ×8; [5] ×2; [4] natural size.

so that the small gaping slit through which the pollen has to be discharged into the air faces upward. Consistently with this fact we find that in Plantains it takes a couple of days to disperse all the pollen. The same category includes the Elms

(*Ulmus*, see fig. 232), the Japanese Bocconia (*Bocconia Japonica*), the Meadow-rues with erect and divergent stamens (*Thalictrum aquilegifolium, T. angustifolium, T. flavum*, &c.) and several species of *Poterium* and *Sanguisorba*. The filaments of Elms are straight at all times, but they elongate shortly before the anthers open to about double their original length, and the dehiscent anthers are then displayed as pairs of gaping valves. In *Bocconia* the anther-cavities are in the form of long narrow niches, and the erect, radiating, filiform filaments vibrate under the slightest breath of wind like the aigrettes ladies sometimes wear on their heads. In the species of Meadow-rue which grows commonly over the lower Alps (*Thalictrum aquilegifolium*), and in the Siberian Burnet (*Sanguisorba alpina*), the stamens are clavately thickened towards the top, and are organized like those of Bocconia in such a manner as to be easily set swinging even when the air is only slightly stirring. The various species of *Plantago, Thalictrum*, and *Ulmus* are also remarkable for the fact that the fissures formed in their anther-lobes during dry weather close up quickly in the event of rain, and remain shut until the rain has ceased and the atmosphere has again become dry.

Fig. 234.—Male Flowers of Yew (*Taxus baccata*).

[1] Anther with closed pollen-sacs. [2] Anther with its pollen-sacs open and empty. [3] Branch whose lower flowers are discharging their pollen. [1], [2] × 2; [3] × 7.

In all the cases discussed hitherto the pollen escapes from the place where it originates into the air direct. But there are also a large number of plants whose pollen falls in the first instance on to some spot within the province of the flowers, where it is protected from becoming wet, and in which it remains for a period of varying duration; nor is it blown away until conditions favourable to its dispersal obtain in the environment. Very different parts of a flower are utilized in this manner as temporary halting-places for the pollen. In Pines and Firs the backs of polliniferous scales subserve this purpose in a curious way. The upper surface of each anther-scale in the Mountain or Dwarf Pine (*Pinus Pumilio*) is slightly excavated owing to the lateral edges being reflexed and the broad

membranous scale in which the connective terminates being turned up, whilst on either side of the middle line there is a shallow trough (fig. 233[1]). It is easy to convince one's self of the fact that these excavations serve for the reception of the pollen which falls from the anthers above them (see fig. 233[2]), and inasmuch as all the anthers crowded together in a particular spike usually open simultaneously, all the scales of the spike in question have their backs covered with the pollen-dust at the same time (fig. 233[3]). As long as there is no wind the pollen rests on the scales where it has been deposited; but the moment a gust of wind shakes the boughs and twigs of the Pine-tree the pollen is removed from its resting-place, and whole clouds of yellow dust may be seen being blown upward from the spikes (*cf.* fig. 233[4]).

The corresponding adjustment in the Yew (*Taxus*) differs to a certain extent from the above which is so characteristic of Pines and Firs. The connective of the anther-lobes in *Taxus* does not terminate in an upturned scale, but in a little circular shield with an crenate margin. The anther-lobes are attached to the under surface or back of this shield (see fig. 234[1]). Moreover, the anthers are united into roundish heads, and the peltate connectives lock closely together like the separate parts of a mosaic, so that the pollen-sacs are not visible superficially. When the pollen has reached maturity and has assumed the form of powder, the pollen-sacs concealed underneath the shields burst open, their walls shrivel, and the anthers have then the appearance portrayed in fig. 234[2]. The shields now resemble cupolas, supported by short columns, and arching over spaces in which is stored a heap of loose powdery pollen. Under the influence of a warm, dry atmosphere the tissues of the shields contract somewhat, and in consequence chinks appear between the shields, and the spherical conglomeration of anthers seems to be rent asunder (see fig. 234[3]). When the branches of the Yew are caused to sway by a gust of wind a portion of the pollen is at once blown out through these chinks in the form of a little cloud. In the evening when the atmosphere becomes damper, as also on dull and rainy days, the shields lock together again, and such pollen as is left is once more inclosed and protected from wet. On the return of warm, dry weather the cracks reappear, and the remainder of the pollen may be shaken out and blown away.

The mechanism which has here been described in the case of the Yew, that being an easily accessible example, is found to exist in its main feature, though with many varieties of detail, in the Juniper, in Cypress, and Arbor Vitæ (*Juniperus, Cupressus, Thuja*). One species of Juniper, viz.: *Juniperus Virginiana*, in which the little heads of stamens are closed when the atmosphere is damp, and open when it is dry, has been already selected for illustration in figs. 226[15, 16, 17, 18], p. 125. Curiously enough, the Planes (*Platanus*), which are not related to the Conifers just referred to, exhibit similar characteristics in the matter of pollen liberation. The stamens have a peltate or pulvinate connective spread out over the anthers, and each stamen, considered by itself, resembles a short peg or nail with a large, thick head. Besides bearing little papillæ, which are looked upon as abortive

petals, the globular receptacle of the inflorescence supports a large number of these peg-shaped stamens. They stand out in all directions from the sphere, and their peltate connectives have their edges in contact as in the case of the Yew. Similarly, also, cavities are formed beneath the roof, composed of the connectives, and serve as temporary resting-places for the pollen-cells when they are discharged

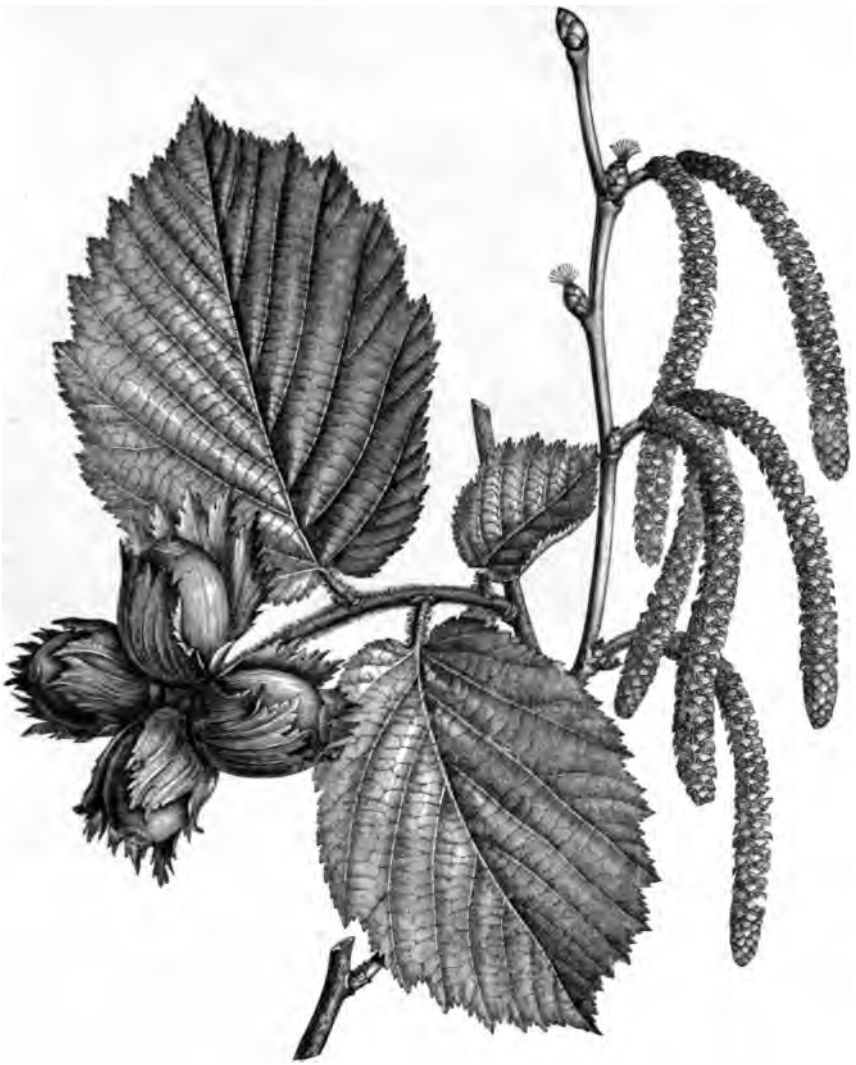

Fig. 235.—Hazel (*Corylus Avellana*) with flowers and fruits.

from the dehiscent and shrivelling anthers. The final process of dispersal of the pollen in the form of dust is, however, essentially different from that which occurs in Yew, Cypresses, and Junipers. In Planes individual stamens fall out of the spherical inflorescence, like bits out of a mosaic, and thus gaps are formed which constitute the means of egress from the cavities filled with pollen-dust. The inflorescences are suspended by long stalks, like big beads on a knotted string

as soon as a wind sets them in motion the pollen is discharged through the gaps in little clouds.

A temporary deposition of the pollen on the backs of the flowers is common to all the numerous trees and shrubs which have their male flowers aggregated in pendent catkins or spikes resembling tassels or fringes in appearance, as, for instance, the Hazel (*Corylus*, see fig. 235), the Alder (*Alnus*, see fig. 228), the Walnut (*Juglans*, see vol. i. p. 742), Birches, Poplars, and Hornbeams. The floral spikes of all these plants are erect at first, and in the form of short, thick cones

Fig. 236.—Curled Pondweed (*Potamogeton crispus*) in the act of pollination.

and cylinders. A short time before the anthers burst the axis of the spike elongates and becomes pendent, causing all the flowers seated upon it to assume an inverted position with their originally upper faces turned to the ground and their backs upwards. The back of each flower is so contrived as to catch the pollen falling from the anthers of the flowers above it, and retain it until the tassels are set swinging by a gust of wind, and the pollen is in consequence dissipated (*cf.* vol. i. p. 741).

Sometimes the hollow upper surfaces of sepals, petals, or bracts serve as landing-stages for the pollen when it is discharged. This is the case, for example, in various species of the Pondweed genus (*Potamogeton*), in the Arrow-grass (*Triglochin*), and the Sea-Buckthorn (*Hippophae*). In the Curled Pondweed (*Potamogeton crispus*), a plant which lives submerged in ponds and slow running

brooks, and in the height of summer raises its flower-spikes above the surface of the water (see fig. 236), the large, fleshy, reddish-brown stigmas are already ripe to receive the pollen at a time when the anthers close beside them are still closed. The perianth-leaves of the flowers concerned are indeed still folded together, and may be seen underneath the four projecting stigmatic lobes which are arranged in a cross, whilst the anthers are hidden beneath the perianth. The shortly-stalked, concave perianth-leaves do not open back until the stigmas have begun to wither. Almost at the same instant longitudinal slits are formed down the large, white anthers, and they are speedily converted into gaping fissures, out of which flows a copious supply of yellow pollen of mealy consistency. If a fresh, dry wind is blowing at the moment of the dehiscence of the anthers part of the pollen is at once carried off from the spikes of the Pondweed as they project above the water; but if a calm prevails a certain amount of the pollen drops into the cavity of the particular perianth-leaf immediately below the anthers. Here the pollen may remain for hours together if there is no wind. It is only blown away by a strong puff of wind, and is then conveyed directly to other spikes projecting out of the water whose flowers happen to be in a much earlier stage of development, the four radiating stigmatic lobes being in a receptive condition, but the anthers yet indehiscent and the perianth-leaves still closed (see fig. 236).

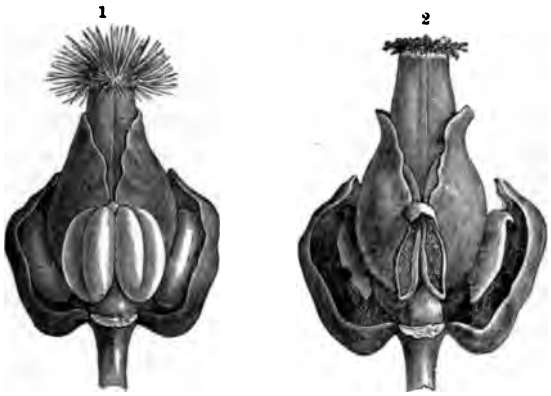

Fig. 237.—Arrow-grass (*Triglochin palustre*).

1 A flower with brush-like stigma already mature; all the anthers still closed. 2 A flower with the stigma withered whilst the three inferior anthers have opened and are depositing their pollen in the concave perianth-leaves at their bases. In both flowers the lower front perianth-leaf has been cut off. × 8.

A still more striking instance of the temporary storage of pollen in concave perianth-leaves is found in the Arrow-grass (*Triglochin*). Here, too, the development of the stigmas precedes that of the anthers by two or three days. During the whole period that the brush-like stigma at the top of the ovary is sound and in a receptive condition the anthers are closed, and they only open when the stigmas have faded and turned brown (*cf.* figs. 237[1] and 237[2]). The stamens, six in number, are in two whorls of three each, situated one above the other (*cf.* vol. i. p. 646), and underneath each stamen there is a deeply-concave perianth-leaf. As soon as the anther opens the pollen rolls into the receptacle thus prepared beneath it, whilst in the meantime the perianth-leaf has moved a little away from the axis and somewhat loosened its connection with it. The pollen rests in its hollow until a puff of wind sets the slender floral spikes swaying to and fro and blows away the pollen. It is a noteworthy circumstance that all six anthers of a flower do not open at once, but that first the lower whorl of stamens comes into play, and that after their pollen has been carried away

by the wind as above described both the empty stamens and the perianth-leaves at their bases drop off. Only after this has happened does the upper whorl of perianth-leaves relax; the anthers of the three upper stamens burst open, their pollen glides into the bowl-shaped perianth-leaves below, and exactly the same process is repeated as took place in the case of the superior whorls.

The case of the Sea-Buckthorn (*Hippophae*; *cf.* figs. 220 [2, 3, 4, 5], p. 109), is worth mentioning as a third example of the same nature. The flowers of this shrub are conglomerated in little tufts on the sides of woody branches. Each male flower is composed of four stamens and two opposite concave scales; the latter have their edges in contact, so that they form a little bladder within which the four stamens are concealed. The pollen is of an orange-yellow colour and mealy consistency, and is set free from the anthers at a time when the bladder is still closed. It falls into the cavity, and is there completely sheltered from rain and dew by the overarching scales. When a warm, dry wind sweeps over the shrubs the bladders open by two opposite chinks, and the pollen is blown out from its resting-place in small quantities at a time. In damp weather the two scales close up quickly and protect what remains of the pollen from wet; on the return of dry weather they move apart again, leaving a free passage for the wind, which then carries off the rest of the pollen. This simple mechanism ensures the safety of the pollen in the event of rain, whilst enabling it to reach the stigmas of neighbouring shrubs whenever the external conditions are propitious.

A close connection exists between these various contrivances to ensure that pollination shall only take place at the best possible moments, and the maintenance of a free passage in the direction in which the pollen is to be transported by the wind, and further between these adaptations and the shape of the stigmas devised for the reception of the pollen. It is obvious that no barrier must be interposed in the path of the little clouds of pollen-dust on their journey to the stigmas. If the flowers of the Arrow-grass, of Pondweeds, or Grasses were wrapped in large foliage-leaves a great part of the pollen would adhere to these leaves and would be as irretrievably wasted as if it had fallen to the ground or into the water. On this account also all flowers which have their pollen blown out of them by the wind are arranged in spikes and panicles at the upper extremities of the shoots and project freely into the air, but are never clothed with a mass of foliage. Particular attention may be drawn to the fact that a large number of plants wherein the pollen is in the form of dust flower before coming into leaf; that is to say, yield up their pollen to the wind at a time when the green foliage is still folded up in the buds or is just emerging from them. The Sea-Buckthorn, the Alder, the Ash, the Elm, the Hazel, the Birch, and the Aspen all flower and discharge their pollen at a season when the branches are bare of leaves (*cf.* the illustrations on pp. 109, 135, 138, 143, and 147). Were these plants to begin to blossom after the complete development of their extensive foliage the wind-transport of the pollen would be rendered

almost impossible. The way to the stigmas would be stopped by innumerable barriers, and the pollen would inevitably be deposited upon these obstacles and stranded.

As regards the stigmas, we find that in plants with dusty pollen they are invariably fashioned so as to catch the dust. In one case they are fleshy and swollen and have the surfaces which are exposed to the wind covered with a velvety coating (see fig. 236), in another they are in the form of tufts of long papillose or capillary filaments, as, for instance, in the Paper Mulberry-tree (*cf.* figs. 229[1] and 229[6], p. 137); sometimes they assume the shape of delicate feathers (*cf.* fig. 231, p. 139), sometimes of camel's-hair pencils and brushes (fig. 237). At the time when pollination takes place they are always fully exposed to the wind and so placed that when the pollen-cells are blown against them they are caught like midges in a spider's web. Yet, in spite of all these contrivances, it would remain very doubtful whether the stigmas would be dusted with pollen through the action of wind were it not for the concurrence of another circumstance. The wind is but an uncertain means of transport, especially in the case of a passive object incapable of exercising any influence on the selection of a route. It is, therefore, important that the pollen should be disseminated broadcast in as thorough a manner as possible, and this is only possible if the number of pollen-cells is excessively large. Supposing that only two thousand pollen-cells were produced in a Nettle-inflorescence and these were surrendered to be the sport of the wind, it would be only by a lucky chance that a single one of these cells would be caught by the stigmas of a plant at a distance of 5 metres; but, inasmuch as the number of the cells constituting the pollen-dust of a Nettle amounts to millions, the probability of successful pollination is increased to a proportionate extent. If the staminiferous flowers of Conifers, Hazels, Birches, Hemp, or Nettles be picked before the dehiscence of their anthers and placed on a suitable substratum until the anthers open, the mass of pollen-dust which is liberated is quite astonishing. It seems scarcely credible that so large a quantity of pollen could have been developed in anthers which are themselves so small, and the apparent anomaly only becomes intelligible when one remembers that the cells were packed closely together in the anthers, but afterwards lie simply in a loose heap. In years peculiarly favourable to the flowering of Conifers vast clouds of pollen are borne on gentle winds through the Pine-forests, and are often swept right beyond them, so that not only the female flowers, needles, and branches of the trees in question are powdered over with the yellow pollen, but also the leaves of adjoining trees and even the grasses and herbs of the meadows around. In the event of a thunder-shower at such a period the pollen may be washed off the plants and run together by the water as it flows over the ground, and then, after the water has run off, streaks and patches of a yellow powder are left behind on the earth, a phenomenon which has given rise on various occasions to the statement that a fall of sulphurous rain has taken place.

DISPERSION OF POLLEN BY ANIMALS.

If this book were ornamented with pictorial initial letters illustrative of the contents of each section, we should have at the head of this chapter a group of flowers with bees and butterflies swarming round them, whilst into the scrolls of the capital would be woven a representation of the quiet life of field and forest as manifested on bright summer days—a subject which plays a prominent part in the poetic descriptions and pictorial art of all unsophisticated nations. Even in these days, pictures of butterflies fluttering about bright-coloured flowers, or of bees engaged in collecting the materials for their honey-combs, still find an appreciative public. Young people especially take pleasure in subjects of the kind, and, since youth never entirely dies out, there will always be people who prefer to see the beautiful lines and tints of flowering meadow and shady wood depicted in miniature than the bold outlines of a landscape. If, however, mere casual observation of the relations between flowers and their insect visitors is sufficient to cause æsthetic pleasure, and has stimulated people of every age and nationality to the production of works of art, it may be imagined how great must be the incentive to scientific study supplied by a deeper insight into these phenomena, and what extreme pleasure is derived from the successful discovery of the reasons for these wonderful relations, and from tracing their connection with other facts of science. It may be confidently asserted that the careful investigation of the processes connected with the visits paid by insects and other animals to flowers has brought the solution of the main problems of modern science considerably nearer, and we have good ground for hoping that the prosecution of these researches will succeed before long in raising the veil which still conceals the truth in the case of a number of unexplained phenomena.

Zoologists are quite justified in their assertion that many of the developments of insects' bodies are correlated with the forms of particular flowers. But equally true is the conclusion to which botanists have arrived that many of the properties of flowers are likewise in correlation with the shape and habits of flower-seeking insects. Now, these flower-loving animals which would perish if for a single year the earth were destitute of blossoms, vary to an extreme degree in size and shape, in the nature of their external coatings, in what they require for nutrition, and in respect of their time of flight, and of a large number of other habits dictated by soil and climate. From the tiny midges to humming-birds, from the thrips, which are scarcely 1 mm. long, and live and die with the flowers, to the gigantic butterflies of Ceylon, Brazil, and New Guinea, whose expanded wings measure 16 cm. across, and which flutter cumbrously from flower to flower, a long and graduated series extends which corresponds with a perfectly similar series in the floral world. The diversities of colour in the creatures which visit flowers, the various kinds of mechanism of flight exhibited by beetles, flies, bees, butterflies and birds, the multiplicity of organs by means of which they extract their food from

the flowers, their means of attachment to the blossoms, their fur and bristles for brushing off the pollen, have all their corresponding variations in form and colouring amongst flowers, and consequently there is an equally long and apparently parallel series in the realm of plants.

Contemporaneously with the opening of the earliest spring flowers occurs the escape of the first pioneer butterflies from their cocoons; the same sunny day which rouses hive-bees and humble-bees from their winter sleep, sees the Willow-catkins protrude from their brown bud-scales and offer their honey and pollen to the world at large. Many flowers which open early in the morning are only visited by particular butterflies which forsake their nocturnal haunts at the same hour; as soon as the flowers close at sunset the insects in question also seek their quarters, fold their wings, and remain the whole night fast asleep. Other flowers do not open till sunset, when day-flying butterflies are already gone to rest, and they are visited by Hawk-moths, Silk-moths, Owlet-moths, and other Noctuæ which have remained throughout the day concealed in shady nooks and commence their ramblings when dusk sets in. These instances of the mutual relations existing amongst vital phenomena obtrude themselves annually on the notice of the most superficial observer, and have been described time after time.

We need not occupy ourselves any longer at the present day with an account of the facts themselves, but rather with the inquiry into the causes both proximate and remote of all phenomena which are presented to our wondering senses. First of all, the question arises: what is it that induces insects and small birds to visit flowers, and what advantage accrues to a plant from the visits with which its flowers are favoured? The answer is, that the inducement is in some cases care of young, in others the desirability of securing themselves against dangers from storms, and, most commonly of all, it is the craving for food. Flowers, however, do not provide animals with breeding-places, with temporary shelter, or suitable nutriment without claiming a reciprocal service, but have their parts so adjusted that their visitors become laden with pollen, which is then transported to other flowers and deposited on their stigmas where it initiates a series of changes resulting in the setting of the seeds. The next few pages will be devoted to the elucidation and proof of this general answer by aid of individual instances.

As regards the choice of nests for their young it has long been known that the nocturnal Lepidoptera of the genus *Dianthœcia*, and also some species of the genus *Mamestra* lay their eggs in the flowers of Caryophyllaceous plants, *e.g.*, in those of the Nottingham Catchfly, the Bladder-campion, Ragged Robin, and Common Soapwort (*Silene nutans*, *Silene inflata*, *Lychnis Flos-cuculi*, *Saponaria officinalis*). The eggs, which are brought forth through a comparatively long ovipositor, produce tiny caterpillars which move about freely in the undivided cavity of the ovary, and there enjoy not only complete shelter but suitable nutriment, for they live on the ovules and young seeds which are seated upon the central placenta situated in the middle of the ovary. When they grow up they bite a hole in the side wall of the ovary, creep through it and descend to the ground, where they pass into the

chrysalis condition. One may see, frequently, on examining the ripe fruit-capsules of the Catchflies, the perforations by which the moth-larvæ have gained their freedom. If the caterpillars of *Dianthœcia* devoured all the seeds in the ovaries, the species of plants frequented by them would derive no benefit, but, on the contrary, an injury from their visits. Owing to the large number of ovules, however, they are very seldom completely destroyed, and even if all the seeds in one of the capsules were to be consumed there would always be other capsules in the same plant which would develop plenty of seeds capable of germination. The majority of the Caryophyllaceous species here in question, the Nottingham Catchfly (*Silene nutans*, see figs. 238 and 239) amongst the rest, flower at night, their blossoms opening at dusk, remaining expanded all night, and closing at sunrise. This is repeated in the case of each flower at least three times. On the first evening the petals which have hitherto been rolled up and folded in the bud, spread themselves out in rays and bend somewhat back (fig. 239); five anthers are rapidly exserted from the middle of the flower, and these soon afterwards dehisce, become covered with adhesive pollen, and remain the whole night in that condition. In the course of the following morning the filiform filaments bearing the anthers belonging to the outer circle of stamens bend back, and the anthers fall off or, less commonly, are left hanging to the ends of the reflexed filaments in the form of empty shrivelled sacs. The next evening the second whorl of stamens included in these flowers comes into play, and just in the same manner as before, five anthers, which dehisce at nightfall, are exserted from the mouth of the flower and expose their pollen. The third day these stamens likewise bend back and usually let their anthers drop, and when dusk sets in the long velvety S-shaped stigmas, which have till then been concealed inside the flower, are pushed out. Certain changes of position affecting the petals proceed simultaneously with these mutations. It has already been mentioned that the petals rolled up in the bud unfold on the first night, and assume a stellate and reflexed attitude. At this time also the flowers emit a delicate perfume like that of hyacinths, which attracts a large number of nocturnal insects, but only lasts from 8 o'clock in the evening till about 3 A.M. At daybreak the petals begin to roll up again, the operation taking place faster when the temperature is moderately high and the sky clear than when the weather is cold and the sky overcast. In the process of involution the petals fall into longitudinal folds and become wrinkled and grooved, so that they hang like five crumpled bags round the mouth of the flower, and

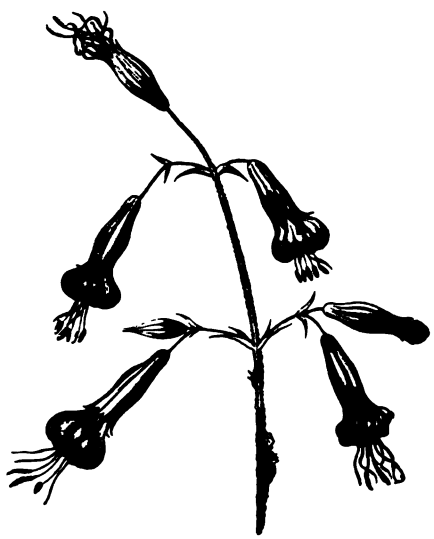

Fig. 238.—The Nottingham Catchfly (*Silene nutans*) in the daytime.

by their appearance might lead one to think that the flower had faded (see fig. 238). But as evening approaches the wrinkles vanish, the petals unfold, spread themselves out into a star, and become slightly reflexed once more. One peculiarity of these flowers is that the inner surface of the petals is white, whilst the outer surface is always of some inconspicuous colour, such as dirty-yellow, greenish, brown, dull red, or ashen-grey. Hence the radiating petals with their white inner surfaces exposed are very striking in the evening darkness, whereas in the daytime the crumpled petals with only their backs visible are anything but conspicuous, and give the impression of being already brown and withered, as may be seen in fig. 238. They are consequently not noticed by insects in the daytime and receive no visits from them.

Fig. 239.—The Nottingham Catchfly (*Silene nutans*) by night; a flower being visited by the moth *Dianthœcia albimacula*.

This appears to be exactly what is aimed at. Such insects as visit flowers by day in order to suck their honey would be the reverse of welcome to the Catchfly. The filaments are reflexed, the anthers shrivelled and empty or dropped, and there is no pollen in the flower to be brushed off. A honey-sucking insect could not either take up or deposit pollen in the daytime, and the honey would therefore be sacrificed in vain. Indeed, the flowers would be worse off inasmuch as, being despoiled of their honey, they would possess one less means of attraction in the ensuing night. On the approach of night the pollen-laden anthers and velvety stigmas appear in front of the entrance to the interior of the flower where the honey is concealed, the scent and white colour act as allurements, and the visits of insects are welcome, provided the size of their bodies is such that they rub against the pollen or stigmas and fly quickly from one flower to another. Those which are too small, or are destitute of wings, are still kept at a distance, this being effected by means of contrivances which will be the subject of discussion later on. Of all the welcome species the best adapted in respect of size and shape of body, length of proboscis, and various other structural characteristics are the Owlet Moths (Noctuæ), and of these in particular those of the genus *Dianthœcia*, one of which is represented as visiting the flower of the Nottingham Catchfly in fig. 239. These little moths pay frequent visits to suck the honey whilst the females also lay their eggs in the flowers. It sometimes happens, too, that the females become loaded with pollen from a flower upon which they have rested and taken a meal of honey, and that afterwards they fly with the pollen to other flowers where, instead of sucking any more honey, they

lay their eggs, and in so doing dust the stigmas with their freight. To sum up, the flowers of the Nottingham Catchfly and of other species of Caryophyllaceæ above referred to are adapted to the small Noctuæ of the genera *Dianthœcia* and *Mamestra*, and are visited exclusively, or, at any rate, principally, by those insects. The Noctuæ obtain honey from them, and the females find in them homes suitable for their eggs. The return made by the moths to the plants consists in the conveyance of pollen from flower to flower and the consequent conversion of ovules into seeds which would not be effected spontaneously.

The relations just described occur also among several other groups of plants and Lepidoptera. A number of species of the small blue butterflies belonging to the genus *Polyommatus* stand in the same relation to Leguminosæ and Rosaceæ. The beautiful *Polyommatus Hylas* visits the flowers of Lady's-fingers (*Anthyllis Vulneraria*) and in doing so transfers the pollen from one plant to another. The female lays her eggs in the ovaries of the flowers she visits, and from the eggs issue caterpillars which feed on the young seeds. When mature the caterpillars forsake the ovaries and retire underground to pass through the chrysalis stage. The same relation exists between *Polyommatus Bœticus* of Southern Europe and the Bladder-Senna (*Colutea arborescens*), between *Polyommatus Arcas* and the Great Burnet (*Sanguisorba officinalis*) and in many other cases; only, besides the butterflies named, others alight with a freight of pollen on the flowers of these plants, but do not lay eggs in the ovaries, and only receive honey in return for their conveyance of the pollen, so that these cases are really only partially of the same category.

On the other hand, the life-history of one of the moths living on the capsule-bearing species of the genus *Yucca*, and named *Pronuba yuccasella*, has been made out, and must here be dealt with in some detail, as it affords one of the most wonderful examples of the dispersal of pollen by means of egg-laying insects. The flowers in all species of *Yucca* are arranged in large panicles (vol. i. fig. 154, p. 659), and each is bell-shaped and suspended at the end of a smooth, green stalk. The perianth-leaves, six in number, are yellowish-white and are consequently visible from a considerable distance in the dusk and on moonlight and starry nights. After the flower-buds open, which happens regularly in the evening, the perianth forms a widely-open bell (*cf.* fig. 240[1]). The dehiscence of the small anthers, which are supported on thick and velvety filaments, takes place simultaneously with the divergence of the petals, and a golden-yellow adhesive pollen is to be seen in the spiral slits of the anthers. Each flower is wide open for one night only; by the next day the free extremities of the six perianth-leaves bend towards one another causing the flower to assume the form of a balloon or bladder with six narrow lateral apertures (fig. 240[1]). In the twilight and by night, numerous small yellowish-white moths (*Pronuba yuccasella*; see fig. 240[4]) which have a metallic glitter in the moonlight flutter about the flowers of the *Yucca* plants. The females penetrate into the interior of the wide-open bells and there endeavour to possess themselves of the pollen, not with a view to devouring it, but that they may carry it away. For this purpose they are furnished with a special implement. The first

joint of the maxillary palp is lengthened to an extraordinary extent, and its inner surface is beset with stiff bristles and can be rolled up like a trunk (see fig. 240[5]). It is used to seize the pollen, to conglomerate it into a ball and afterwards to hold

Fig. 240.—Transport of Pollen by Egg-laying Insects.

[1] Branch from the inflorescence of *Yucca Whipplei*; the middle flower open, that beneath it was open the previous night and is now closed again, the rest of the flowers in bud. [2] Single flower of the same plant visited by a moth of the species *Pronuba yuccasella*; the three front perianth-leaves removed. [3] Stigma of *Yucca Whipplei*. [4] *Pronuba yuccasella* flying to a flower of *Yucca Whipplei*. [5] Head of *Pronuba yuccasella* with a ball of pollen held by the coiled maxillary palp. [6] Twig with inflorescence of *Ficus pumila*; the urn-shaped inflorescence (or synconium) cut through longitudinally. [7] Single female flower from the bottom of the synconium of *Ficus pumila*. [8, 9] Stamens of the same plant from the upper part of the synconium. [10] Synconium of *Ficus Carica* full of gall-flowers produced by *Blastophaga*, cut through longitudinally; near the mouth of the cavity is a Fig-wasp (*Blastophaga grossorum*) which has escaped from one of the galls. [11] Synconium of *Ficus Carica* full of female flowers, cut through longitudinally; near the mouth of the cavity are two Fig-wasps, one of which has already crept into the cavity whilst the second is about to do so. [12] Male flower. [13] Long-styled female flowers of *Ficus Carica*. [14] Gall produced from a short-styled gall-flower. [15] *Blastophaga grossorum* escaping from a gall. [16] A liberated *Blastophaga*. [17] The same magnified. 1, 2, 4, 6, 10, 11, 16, natural size; 3 × 2; 5 × 20; 7, 8, 9, 12, 13 × 5; 14, 15, 17 × 8.

it. In a very short time a moth collects by its means a ball of pollen, which is held by the rolled-up palpi close underneath the head and resembles a great crop. Laden with this lump of pollen, which is sometimes three times as large as its head, the

moth abandons the despoiled flower and seeks another forthwith. Having found one, it circles nimbly round it, making a sudden spring off and on, and ends by settling on two of the thick reflexed filaments, sprawling its legs out upon them. It then seeks to reach a favourable spot on the surface of the pistil with its ovipositor and there deposits its eggs. The ovipositor is composed of four horny bristles, and is adapted to pierce through the tissue of the pistil. After the eggs are laid and the ovipositor is withdrawn, the moth darts to the top of the infundibuliform stigma (fig. 240 [3]), unrolls its trunk-like palpi, and stuffs the pollen into the stigmatic funnel, moving its head to and fro repeatedly during the operation (fig. 240 [2]). It is alleged that the same moth repeats the processes of alternately laying eggs and stuffing the stigma with pollen several times in the case of the same flower.

Most of the eggs introduced into the pistil are deposited in the vicinity of the ovules. They are of oblong shape, narrow and transparent and increase rapidly in size, soon revealing in each a coiled-up embryo. On the fourth or fifth day the larva is hatched and at once begins to devour the ovules in the cavity of the ovary. Each grub requires from 18 to 20 ovules to nourish it during the period of its development. When it is grown up, it bites a hole in the still succulent wall of the ovary, crawls out through the aperture, lets itself down to the ground by a thread, burrows into the earth and spins an oval cocoon underground in which it remains till the following summer. Fourteen days before the time of flowering of the *Yucca*, it begins to show signs of life, and the moment the flowers of that plant open the silvery moths escape from their pupal envelopes.

An important element in the interpretation of the relations subsisting between the *Yucca* and the *Yucca*-moth is the fact that without the assistance of insects the sticky pollen of the plant in question could not get to the stigma. In the case of *Yucca aloefolia* alone there seems to be sometimes a transfer of pollen to the stigma through the instrumentality of the petals or of the elongating filaments; but in most species of this genus, that is to say, in those wherein the fruit is capsular, this certainly does not take place. With the exception of the moth referred to, insects but seldom fly to them, and those which alight by chance on the flowers do not cause a deposition of pollen on the stigmas. If it were not for the transport of the pollen by *Pronuba yuccasella* the ovaries and ovules of *Yucca* would not ripen into fruits and seeds. As a matter of fact, all the fruits of the capsular species are rendered abortive if moths are kept away from the flowers by means of a gauze covering. Also, in gardens where there are no *Yucca*-moths, the production of fruit is suppressed. *Yucca Whipplei*, which in California, its native land, is visited by a particular moth and develops an abundance of dehiscent capsular fruits, has repeatedly flowered in the Botanic Gardens of Vienna, but the moth does not exist in the gardens, and, in consequence of its absence, not a single fruit has ever ripened there. On the other hand, it is ascertained beyond a doubt that the grub of the moth in question lives exclusively on the young seeds of these species of *Yucca*, so that one is forced to the conclusion that the moth stuffs the

pollen into the stigma in order that its grubs may be supplied with the nutriment requisite for the preservation of the species—nutriment which would not be forthcoming unless the ovules were fertilized.

This inference does not, of course, involve the assumption that the operations in question are carried out deliberately by the moth with an intelligent foresight of the results. But there is no objection to our looking upon the habits of these insects as unconsciously purposeful. The stuffing of the pollen into the stigmatic funnels is neither more nor less wonderful than the fact that in remote valleys where the population is very sparse and there are very few vegetable gardens, the cabbage white butterfly often flies miles away to look for cabbages upon which it may lay its eggs so that the grubs may find the food that suits them the moment they are hatched. Equally marvellous, too, is the case of many kinds of caterpillar which spin their cocoons on the bark of trees, and cover the structures wherein they are subsequently to undergo transformation into the chrysalis-state with lichens and fragments of bark, that their temporary resting-place may not be noticed by insectivorous birds; and again the same sort of phenomenon encounters us in the case of the caterpillars which live in the interior of the hard parts of plants, and before transforming themselves into pupæ make a special exit ready for the soft and delicate imago subsequently to be liberated.

It must be observed that the grubs of *Pronuba yuccasella* do not eat up all the developing seeds of the ovary in which the moth lays her eggs. There are about 200 ovules in each ovary. Even if half or two-thirds of them are consumed, there is still a sufficient number of uninjured seeds left to be scattered abroad when they have reached maturity, whereas without the intervention of the moth not a single seed capable of germination would have been produced. Whether or not symbiosis with moths also occurs in the species of *Yucca* bearing berries has not been ascertained for certain; but seeing that the berry-producing species, *Yucca aloefolia*, *Y. Treculeana*, &c., have been found to have holes in all their mature fruits—at least when they are growing in their native countries (Florida, Carolina, Mexico, Louisiana, Texas)—and other traces have been discovered pointing to their having been occupied by caterpillars, the probability is very strong that such is the fact.

Still more remarkable than the relation between the genus *Yucca* and its companion moth is that existing between Fig-trees and certain small wasps of the group of the Chalcididæ. To understand the relation clearly, it is first of all necessary to examine the construction of the inflorescence in the Fig. Looking at a fig that has been cut open lengthwise, as is shown in fig. 240 [6], it is observed that it is not a simple flower, but rather a whole collection of flowers inclosed in an urn or pear-shaped receptacle. These pear-shaped shoots are in reality hollow inflorescences bearing numerous flowers on their inner walls. Each fig is termed a synconium. The orifice of the urn is very small, and is further straitened by the presence of small leafy scales. The flowers, which are very simple in structure, almost fill the entire cavity; they are of two kinds, male and female.

Each male flower is composed of one or two—rarely from three to six—stamens, which are supported by scales, and are borne on a short stalk (fig. 240[12]). In many species, as, for instance, in *Ficus pumila*, the stamens are spoon-shaped and have the anthers imbedded in the concavity of the spoon (figs. 240[8] and 240[9]). The female flowers possess a unilocular ovary containing a single ovule. The style is inserted rather to one side of the ovary and terminates in a stigma, which is variously formed. At the base of the ovary are to be seen a few small scales which vary in number, and may be regarded as the perianth (see figs. 240[7] and 240[13]). Many species have two kinds of female flower in the same urn or synconium, viz. some with long styles and developed stigmas, and some with shorter styles and abortive stigmas. The latter are called gall-flowers for a reason that will presently be explained (fig. 240[14]). The relative distribution of male and female flowers is very different in different species. In the inflorescences of the India-rubber Fig (*Ficus elastica*), figured on p. 755, vol. i., the male and female flowers are apparently mixed together promiscuously; in that of *Ficus pumila* (fig. 240[6]) female flowers only are found in the lower part of the cavity, and only male flowers near the mouth. This distribution is the most usual, but yet another difference exists in respect of the number of male flowers. In the synconia of many species the male flowers occur in large numbers near the orifice, whilst in others there are very few—indeed it even happens sometimes that there is an entire absence of male flowers in one inflorescence or another. In many species some individuals only produce inflorescences containing female flowers, and other individuals inflorescences with male flowers near the orifice and with female flowers lower down. But the most remarkable circumstance of all is that in the inflorescences of many species all or most of the female flowers below the male ones are transformed into gall-flowers. This is the case, for instance, in the common Fig-tree (*Ficus Carica*) cultivated in Southern Europe, a species which includes two kinds of individuals, viz. those whose inflorescences contain female flowers only, and those whose inflorescences contain male flowers near the opening and gall-flowers lower down (*cf.* figs. 240[10] and 240[11]). The former individuals are known by the name of *Ficus*, the latter by the name of *Caprificus*.

We have now to consider what may be the meaning of the gall-flowers. As the name indicates, not fruits but galls are produced from these modified female flowers, and this happens in the following manner. There is a small wasp belonging to the Chalcididæ, a family of Hymenoptera (*cf.* fig. 240[16] and 240[17]), already referred to as *Blastophaga grossorum*, which lives upon the Fig cultivated in the south of Europe. This insect passes into the cavity of the inflorescence through the orifice, and there sinks its ovipositor right down the style-canal of a flower, and deposits an egg close to the nucellus of the ovule. The white larva developed from the egg increases rapidly in size and soon fills the entire ovary whilst the ovule perishes. The ovary has now become a gall (fig. 240[14]). When the wasps are mature they forsake the galls. The wingless males are the first to emerge, and they effect their escape through a hole which they bite in the gall. The females remain a little

longer in their galls and are there fertilized by the males. Afterwards they come out also (*cf.* fig. 240[15]), but only stay a short time within the cavity of the inflorescence, issuing from it as soon as possible into the open air. They accordingly crawl up to the mouth of the inflorescence, and in doing so they come into contact with the pollen of the male flowers and get dusted all over the body—head, thorax, abdomen, legs, and wings. After squeezing through between the scaly leaves at the mouth of the inflorescence, and having at last reached the outside, they let their wings dry and then run off to other inflorescences on the same or on a neighbouring Fig-tree. I say "run" advisedly, for they but rarely make any use of their wings in this act of locomotion. They now seek exclusively inflorescences which are in an earlier stage of development, that they may lay their eggs in the ovaries. Having found such an one they crawl to the opening and slip between the scales into the interior. Sometimes their wings are injured in the act of entering, indeed, the wings are occasionally broken off altogether, and are left sticking between the scales near the aperture.

Once inside the inflorescence, the wasps immediately devote themselves to laying eggs, and in the process are of necessity brought into contact with the stigmas of female flowers. The wasps are still powdered over with the pollen from their birthplace, and it is now brushed off on to the stigmas, which are thus pollinated from another inflorescence. If the pollen is deposited on normal pistilliferous flowers the latter are able to develop seeds endowed with the power of germination; if it falls on gall-flowers it is, as a rule, ineffectual, because the stigmas are more or less abortive. Moreover, no seeds are formed in these gall-flowers, owing to the eggs of the wasp being laid in their place. In those species of Fig in which gall-flowers are not specially provided, the eggs are laid in a certain proportion of the normally-developed female flowers. It has, however, been observed in the case of the Common Fig (*Ficus Carica*) that eggs of *Blastophaga grossorum* laid in ordinary female flowers do not come to maturity, or, in other words, that a normal female flower is not converted into a gall, even if the wasp in question sinks its ovipositor into it and deposits an egg in the interior. For the style of the normal female flower of *Ficus Carica* (fig. 240[13]) is so long relatively to the ovipositor of *Blastophaga grossorum* that the egg cannot be inserted quite into the ovary, but is left at a spot which is not favourable to its further development and there perishes. The gall-flowers of this species of Fig, with their short styles (fig. 240[14]), are, on the other hand, pre-eminently adapted to the reception of the egg at the spot where the ovule would otherwise develop, whilst at the same time they are not adapted to the production of seeds capable of germination, since no pollen-tubes can develop upon their abortive stigmas. Evidently we have here a case of complementary functions or division of labour in accordance with the following plan. The wasps which deposit their eggs in the figs carry the pollen both to the short-styled gall-flowers and to the long-styled ordinary female flowers, and attempt to lay their eggs in both kinds of flower. The gall-flowers are prepared expressly for the reception of the wasps' eggs, and young wasps actually develop in them; but their

stigmas not being adapted to the reception of pollen they do not promote the growth of pollen-tubes, and no fertile seeds are produced. On the other hand, pollen-tubes develop on the stigmas of the long-styled flowers, and the latter produce fertile seeds; but the long-style prevents the proper placing of the wasps' eggs, and consequently galls are never or very seldom produced in connection with these flowers.

It would take too long to discuss all the numerous diversities which have been observed in other species of Fig, even if they were known with sufficient accuracy to admit of a general survey. We will only mention that there are approximately 600 species of *Ficus*, which are distributed over the tropical and sub-tropical regions of both the Old and the New Worlds, and that up to the present time nearly 50 species of small wasps of the genera *Blastophaga*, *Crossogaster*, *Sycophaga*, and *Tetrapus* have been identified as effecting the transference of pollen from one inflorescence to another in the various species of Fig. Thus, for instance, *Blastophaga Brasiliensis* has been identified in the inflorescences of seven different kinds of Fig-tree. For the most part each species of Fig has its own particular wasp; only in extremely rare instances have two different species of wasp been found in the inflorescences of one and the same species of Fig.

In Southern Italy and other parts of Southern Europe where the Fig has been extensively cultivated for ages, the majority of the trees planted are *Ficus*-individuals, *i.e.* such as have female flowers only in their inflorescences, these yielding the best and juiciest figs. Fig-plants of the form known as *Caprificus*, which, besides male flowers, contain only gall-flowers in their inflorescences, are not cultivated, because most of their figs dry up and fall off prematurely. A few specimens of *Caprificus* are reared here and there in order that their inflorescences may be artificially transferred to the branches of the *Ficus*-trees. The process of transference is called *caprification*, and the growers believe that the figs of *Ficus* are improved by the wasps which come out of the *Caprificus*-inflorescences and enter those of the *Ficus*. But this opinion, though very wide-spread amongst cultivators and peasants, is not correct. The figs of *Ficus* do not require the intervention of wasps to become sweet and juicy. As a matter of fact, *Ficus*-inflorescences which have been entirely unvisited by wasps and have developed no fertile seeds in their little fruits, ripen into excellent eating figs, and innumerable quantities of the figs sold come from trees and from districts where no process of caprification is employed. It seems, therefore, that the use of caprification must be traditional and have originated at a time when growers were not only concerned with the production of good fruit but of fertile seeds also with a view to the multiplication of the plants. At the present day Fig-trees are no longer raised from seed but from cuttings, and caprification is consequently superfluous. Nevertheless the country people persevere with the old custom in spite of their ignorance of its real significance.

Flowers and floral envelopes are comparatively seldom called upon to act merely as a shelter for the night, or as a temporary refuge. Most bees and wasps have

their own homes which are furnished with safe retreats, and to these they withdraw at dusk and in bad weather, and butterflies, for the most part, are afraid to seek the interior of flower-bells or funnels for any length of residence partly because of their relatively large wings, which are liable to be injured in such confined quarters, and partly because in case of danger a rapid escape from the inside of a flower would be scarcely possible. Only beetles, flies, and Hymenoptera of the genera *Meligethes*, *Melanostoma*, *Empis*, *Andrena*, *Cilissa*, and *Halictus* need be mentioned; they are essentially nomadic in their habits, not possessing homes of their own or any settled night-quarters, but are satisfied with second-rate shelter, and usually pass the night wherever they have spent the day. If there should happen to be flowers there which offer agreeable food in addition to a warm retreat so much the better. Doubtless it is for these reasons that the honey-bearing blossoms of the Bell-flowers (*Campanula*) and the Foxglove, the interiors of which after sundown have a somewhat higher temperature than the environment (*cf.* vol. i. p. 500), are especially favourite shelters on cold nights. The large capitula of *Crepis grandiflora*, and of several other Composites whose outer ligulate flowers close in the evening, are also sought after by small beetles (*Cryptocephalus violaceus*, *Meligethes æneus*) and little dark-coloured bees (*Panurgus ursinus*) to serve as nocturnal refuges, because a higher temperature prevails at night inside the closed capitula than outside. At sunrise they abandon their night-quarters, and in doing so probably—in some cases inevitably—brush off some of the pollen which they carry away and take with them on subsequent visits to other flowers.

Sometimes insects remain in comfortable quarters of the kind not only during the night but also during the day, and even for several days. When once the small beetles of the genera *Anthobium*, *Dasytes*, and *Meligethes* have ensconced themselves in the interior of the flowers of Magnolias or Gentians (*Magnolia obovata*, *M. Yulan*, *Gentiana acaulis*, *G. ciliata*, *G. Pneumonanthe*, &c.), they do not abandon this comfortable home till the third day. This is also true of the rose-chafers (*Cetonia*), which have a preference for the flowers of *Magnolia grandiflora*. They usually force themselves into the youngest flowers which are only just open and take their fill of the sweet juices exuding on and between the stigmas. Later on they devour also some of the pollen as it is liberated from the anthers and drops upon the petals. When the Magnolia-flowers open under a bright mid-day sun, the Cetonias keep still and warm themselves in the sunshine, and when evening comes, and the upper petals close up, they have no inducement to leave the quarters they have chosen, for the temperature rises in the inclosed space during the night from five to ten degrees Centigrade above the temperature outside, and, besides, the Cetonias are here completely sheltered from the attacks of nocturnal animals. Thus they stay in the flowers until the petals fall off and leave them exposed to the air. The flowers of the Opium Poppy (*Papaver somniferum*) are likewise sought out by flies and beetles as soon as they open, and are not deserted until the petals drop. The sojourn is, however, much shorter than in the case of Magnolia-flowers owing to the fact that the Poppy only closes once for the night and loses its petals the very next day.

In the examples above referred to the insects are not forcibly retained in the flowers, for in fine weather the flowers of Gentians, Magnolias and Poppies are as wide open as they can be. But there are also cases where insects, after slipping into a floral cavity for shelter, are kept there for a time imprisoned. This remarkable phenomenon is exhibited especially by the Aroideæ and Aristolochiaceæ. In many Aroideæ (*Arum*, *Dracunculus*, *Helicodiceros*, &c.), of which *Arum conocephaloides* (fig. 241) may be taken as a type, the ensheathing spathe widens out above, whilst below the middle there is a decided constriction, and the lowest part expands into a barrel-shaped receptacle. The temperature inside the cavity is always considerably above that of the environment, and ranges not infrequently from 30° to 36° C.; in the spathes of the Italian Arum (*Arum Italicum*) a temperature of 44° C. has even been recorded (see vol. i. p. 501). All these Aroideæ have an offensive odour of putrefaction, and by this very property attract a number of animals which live on dead bodies and other decaying matter. These creatures settle on the projecting end of the spadix and climb down it into the barrel-shaped cavity, where they find a warm habitation and in addition a supply of food in the thin-walled succulent cells lining the interior. At the part where the spathe is constricted the spadix is encompassed by a ring of stiff bristles, which form a contrivance like a lobster-trap. The points of most of the bristles are curved downwards, so as to allow the insects to climb down into the chamber but prevent their egress. It is not till some days later that the bristles become limp, the constriction in the spathe is loosened and expanded, and the captives are able to leave their temporary prison, and by that time the pollen has been liberated from the anthers and covers that region of the spadix which bears the male flowers; it is thus impossible for insects to climb up the spadix without first becoming loaded with the pollen lying in their way, and they afterwards carry it to other younger flowers. In *Arum conocephaloides* (fig. 241) there are two rings of bristles, one above the other. The upper hairs relax later than the lower ones, and when, after the latter have

Fig. 241.—*Arum conocephaloides*, with the front wall of the spathe removed. On the lowest part of the spadix are the female flowers, above them the first ring of bristles, next the male flowers, and then a second ring of bristles. At the bottom of the cavity are a number of midges belonging to the genus *Ceratopogon* whose escape is prevented by the stiff deflexed points of the lower ring of bristles.

become flaccid, midges that have been imprisoned at the bottom of the cavity pass into the upper story, they are kept there for a time by the upper bristles, which are still rigid, so that the insects knock against the male flowers and must cover themselves with pollen. Finally, when this object is achieved, the upper bristles also relax and the midges are allowed to escape.

It is astonishing what a large number of insects and what a variety of different kinds find a home in the flowers of Aroideæ. The smaller Aroids, such as *Arum maculatum*, widely distributed in Europe, are sought chiefly by tiny midges of the species *Psychoda phallænoides*, and it is not uncommon to find several hundreds of them in the cavity of a single spathe. In the receptacle formed by the spathe of an *Arum conocephaloides*, planted in the Botanic Gardens of Vienna, three species of small black midges of the genus *Ceratopogon* had congregated, and were present in such large numbers that when one of the spathes was opened artificially a whole swarm flew out. A second spathe of the same plant, which was immersed in alcohol and subsequently opened, was found to contain nearly a thousand midges of the kind. In the Italian Arum (*Arum Italicum*) also as many as sixteen different species of flies, mostly of the genera *Chironomus*, *Limosina*, *Sciara*, and *Psychoda*, have been found in a single spathe. Another Aroid, *Dracunculus crinitus*, is sought principally by large flies belonging to the species named *Somomyia Cæsar* and *Anthomyia scalaris*. In the receptacles formed by the spathes of the *Dracunculus Creticus*, which has flowered in the Botanic Gardens of Vienna, various carrion-beetles (*Aleochara fuscipes*, *Dermestes undulatus*, *Saprinus nitidulus*, &c.) had collected, besides numerous green-gilded flies of the genera *Anthomyia*, *Lucilia*, and *Somomyia*; and in the sheathing-bracts of *Dracunculus vulgaris* which grows in Italy scarcely anything but carrion-beetles of the genera *Dermestes* and *Saprinus* have been observed. A single spathe of the last-named plant was once found to contain more than 250 carrion-beetles belonging to eleven different species.

The flowers of the Birthwort genus (*Aristolochia*) bear a surprising resemblance to the spathes of Aroideæ, their perianths being, like aroid spathes, divided into three regions. First of all, there is the limb, which in the European species has the form of a trumpet, and in the tropical species of America assumes many other curious shapes, as, for instance, that exhibited by *Aristolochia ringens* (fig. 242), where it is drawn out into a boat-shaped under-lip with an upper-lip arching over it. Next comes a tubular median portion, which is furnished with various contrivances to prevent the egress whilst permitting the entrance of creatures seeking shelter. Lastly, there is an enlarged basal portion like a bladder or pouch wherein the stigma and anthers are situated, and which constitutes the goal of the insect-visitors. On a future occasion it will be necessary to enter more fully into the manner in which the insects that creep into the pouch take up and afterwards deposit the pollen, and it will therefore be sufficient to mention here that they are kept prisoners there until the anthers have opened. When dehiscence has taken place, and not before, the tubular middle region undergoes certain changes which make it possible for the captives to escape from their temporary dungeon.

For flowers to serve as refuges and nocturnal haunts for insects they need not necessarily be fashioned into hollow receptacles, pouches, bells, or anything of the kind, as is proved by the following observation. In my garden the flowers of plants of *Phlox paniculata*, indigenous to North America, and of the Canadian Golden-rod (*Solidago Canadensis*), which bloom simultaneously in the autumn, were visited by numberless flies—particularly by the large bee-like *Eristalis arbus-*

Fig. 242.—*Aristolochia ringens.* (After Baillon.)

torum—which feasted on as much of the pollen as was accessible to them. By day they stayed as readily on the Phlox-flowers as on the Golden-rod; but as night approached they one and all migrated to the Golden-rod. Not a single fly remained on the Phlox, whereas the great bunches of Golden-rod capitula were covered with hundreds of flies. On the following night, which was still and cold, I examined the flowers by the light of a lantern and found that less dew was deposited on the flowers of the Golden-rod than on those of the Phlox, and this led me to conjecture that the temperature of the former flowers had risen in the night above that of the surrounding atmosphere. And this turned out to be the case. A thermometer inserted in the middle of the inflorescence of the Golden-rod,

which was in full flower, recorded a temperature about 2° higher than the environment, and probably there would have been a still greater difference if the form and disposition of the capitula had not been peculiarly unfavourable to the retention of the warm layer of air in immediate contact with the flowers. The inflorescences of the Phlox exhibited no rise of temperature, but, on the contrary, a fall of 1·5° as compared with the surrounding atmosphere, and they were copiously bedewed. Thus the flies had selected a relatively warm place for their night's rest, although it could not really be called a shelter. As the pollen in the Golden-rod is pushed during the night out of the tube formed by the anthers, the flies found on awaking next morning their meal again ready for them, and it was evidently impossible that they should leave their nocturnal resting-place without first smearing themselves over with pollen.

ALLUREMENTS OF ANIMALS WITH A VIEW TO THE DISPERSION OF POLLEN.

Next to honey pollen is the principal food which animals seek for in flowers. There are some plants from which honey is entirely absent, and which offer only pollen to the food-seeking animals. Such, for example, are the Poppy (*Papaver*), Traveller's Joy (*Clematis Vitalba*), Pheasant's Eye (*Adonis*), and several Anemones (*Anemone alpina, baldensis, sylvestris, Hepatica*, &c.), the numerous Cistuses and Rock-roses (*Cistus* and *Helianthemum*), and Roses (*Rosa*). They all agree in this: that their flowers when open stand erect and have a star-shaped or cup-like form, so that the pollen falling out of the anthers is not lost, but remains for some time on the concave upper surface of the petals. This is especially noticeable in flowers of the Poppy family (*Eschscholtzia, Glaucium, Roemeria, Argemone*; *cf.* fig. 222[1] p. 112, and fig. 243). In comparison with the honey-producing flowers, to be described later on, they always appear to have a simpler construction, which is accounted for by the fact that they have no need of special contrivances for the secretion and storing or protection of honey.

The flowers of these plants are eagerly sought for by little beetles of the genera *Anthobium, Dasytes* and *Meligethes*, and it is no uncommon thing to find in a single Cistus or Rock-rose flower, half a dozen *Dasytes* greedily devouring the pollen. Along with the beetles numerous flies also visit these honeyless flowers for the sake of the pollen, more especially certain Ruscidæ, Stratiomyidæ, and Syrphidæ, which seize the pollen-cells with the terminal lobes of their mouth-parts, bruise them thoroughly, and swallow them bit by bit. Besides these, certain Hymenoptera, *e.g.* species of *Prosopis*, and also Thrips (*Thrips*), are eaters of pollen, and if they establish themselves in great numbers can in a short time almost entirely clear away all there is to be found.

It is well known that bees and humble-bees collect pollen in large quantities and carry it to their nests as food for the larvæ. The collecting is carried on by means of specially constructed hairs and bristles, which clothe various parts of the body, particularly the abdomen and the terminal segments of the hind-legs, and

which are sometimes found united into a thick fur, sometimes arranged in regular rows or bands, or grouped into brushes. Some of the hairs are soft and flexible, like delicate little feathers, and when these structures are crowded close together, they act just like a dusting-brush. The pollen over which they have swept, and with which they have become covered, remains hanging between the feathers, from which it can easily be removed afterwards. Other hairs, as already mentioned, are short and stiff, and resemble eyelashes or bristles, arranging themselves in regular rows, so as to form small besoms. In bees and humble-bees these brushes occur on the end-segments of both hind-legs, while in species of *Osmia* only a single brush is formed on the lower side of the abdomen. When these insects stroke the pollen-covered anthers, or the petals on which the loose pollen has fallen, with their legs or abdomen, they remove the pollen with the small brushes and the chinks between the bristles are quite filled with it. Moreover, the bees and humble-bees, with the assistance of the brushes on the terminal segments of their hind-legs, are able to comb and sweep off the pollen which was imprisoned in the soft hairs of their own fur, and thus these brushes form excellent collecting apparatus. In addition, these insects have special contrivances on their legs which have been compared to little baskets; they are smooth, sharply-defined hollows, hedged in by stiff rod-like bristles, in which the pollen, pressed into clumps and pellets, is packed up to be carried home. Many of these Hymenoptera moisten the pollen which they wish to collect with honey-juice, especially if it is powdery or dust-like, so as to be able to knead it into the little baskets. For instance, when the bees wish to obtain the pollen of the Plantain (*Plantago*) as it emerges from the clefts of the anthers, they eject on it first of all some honey from their extended sucking-tube, by which means the loose mass becomes coherent and adapted for collection. It also frequently happens that the loose pollen to be collected is already provided with juices from the perforated, turgid tissue of the neighbouring petals. If the pollen is sticky provision of this kind is not needed. The slightest disturbance and the most delicate touch are then sufficient, and the pollen adheres to the body of the insect, even the smooth hairless parts of the thorax, the abdomen, and the legs being covered with it.

Fig. 243.—Honeyless Flower of *Argemone Mexicana* with abundant pollen.

Since the sole use of insect-visits to flowers is the transference of the pollen from one flower to another, it is evident that some restriction must be placed upon its too extensive demolition. As a great part of the pollen can always be eaten in the flower, or carried off to the nest as food for the larvæ, it is necessary that some should remain adhering to the body of the visitor, so that the stigmas of other flowers may be adequately provided. This necessity is excellently met by the

superfluity of pollen. All flowers which contain no honey and offer only pollen as food for the insects, *e.g.* those of Cistuses and Roses, of Poppies and Clematises are characterized by a large number of stamens containing so much pollen that in spite of the extensive depredations of the insects, the necessity of pollinating the stigmas is always provided for. The pollen-eating beetles, after visiting such flowers, are always powdered all over with pollen, and as they cannot immediately rid themselves of that which clings to their thorax, abdomen, wing-cases, and legs, when they leave the flowers, they invariably carry it to other flowers. The bees and humble-bees also, which enter such flowers to collect pollen, come out covered as if with flour, and when subsequently they set to work energetically with their leg-brushes to clear the dust from their fur, there always remains behind enough to give the stigmas of other flowers their portion when they next visit them.

Flowers which conceal honey in their depths are very economical with their pollen, and in them care has been taken that it shall not be squandered or uselessly scattered. Animals which frequent flowers poor in pollen are, moreover, vigorous honey-suckers and do not attempt either to eat the pollen or to collect and carry it into the nest for their brood. Involuntarily, they become streaked and clothed with pollen, a state of affairs not always agreeable to them. At the same time it cannot be very disagreeable, for the animals may be seen immediately after flying out of the pollen-strewing flowers as if frightened, entering flowers of the same species in the next moment where they will experience the same treatment. It would indeed be strange if the same flowers should on the one hand have such contrivances as will allure insects in order that they may transfer the pollen from plant to plant, and on the other hand be so arranged as to shock these laden and attracted guests, and disincline them to further visits. Such a contradiction never does occur in the flower-world, but all the contrivances connected with the transference of pollen display a harmony which fills those who busy themselves with these phenomena with astonishment and admiration.

The dusty, flour-like coatings which are observed on the flowers of some Orchids, particularly of the genera *Eleanthus* and *Polystachya*, are very similar to pollen in outward appearance, but in reality wholly different. They consist of masses of loose, round cells which lie in rows like necklaces of pearls on the upper side of the young petals. As a rule, this covering occurs only on the unpaired leaf of the Orchid-flower known as the lip, which thus resembles a tiny cup filled with flour. The loose cells, which look like flour or dust, contain starch, sugar, oil, and albuminous compounds, and so form an excellent food, serving, just like the pollen-cells, to allure and please the insects.

For the most part these dusty, flour-like coatings are rare. It more frequently happens that rows and masses of cells which project from the surface of certain parts of the flower, appearing to the unaided eye as papillæ, hairs, swellings, and warts, are offered as food to these flower-visiting insects, and must therefore be reckoned so far as allurements. In the flowers of the Portulaca (*Portulaca oleracea*) there is a ring-shaped cushion covering the spherical ovary, from its inner

edge spring the stamens, and from its outer margin the petals. Between these two floral whorls the fleshy cushion is seen to be beset with clear, diaphanous papillæ, which, indeed, secrete no juice, but are nevertheless sucked by small insects visiting the flowers, and are sometimes actually eaten. The same is true of the delicate hairs which beset the staminal filaments of the Pimpernel, Mullein, and Spiderwort (*Anagallis*, *Verbascum*, *Tradescantia*), and which under the microscope appear to be turgid cells arranged singly or in rows just like the hairs which clothe the bottom of the hollow perianth-leaf in the flower of the Lady's-Slipper Orchid (*Cypripedium*). In several species of the genus *Lysimachia* (*Lysimachia thyrsiflora*, *ciliata*, &c.), the ovary is covered with small warts whose juicy cells are sucked or devoured by animals; and in the flowers of the Snowflake (*Leucojum*

Fig. 244.—Flowers of the Snowflake (*Leucojum vernum*).

[1] Seen from the side. [2] The front part of the flower cut away and the remaining part of the perianth spread out in one plane. Round the style is a cushion of soft tissue which secretes no honey. (Both figures somewhat magnified.)

vernum; *cf.* fig. 244), there is a cushion-like mass of cells surrounding the style, whose significance is identical with that of the small warts just mentioned. Numerous Orchids, too, viz. *Odontoglossum*, *Oncidium*, and *Stanhopea*, bear fleshy swellings, pegs, and combs on their perianths which admit of a similar interpretation.

It also often happens that certain portions of flat petals consist of a cell-tissue which can be easily perforated and sucked by the mouth-apparatus of insects. Such parts are usually distinguished from their surroundings by their greater brilliancy, and one might suppose that this was due to a thin layer of fluid, although this is not really the case. Especially noticeable in this respect are the flowers of *Centunculus minimus*, a tiny Primulaceous plant, whose cup-shaped corolla is carpeted at the bottom with slightly-arched, large, juicy, superficial cells, which glitter like silver in the sun. The petals of the Bloodwort (*Sanguinaria*), of the St. John's Wort (*Hypericum*), of the Laburnum (*Cytisus Laburnum*), of *Spartium*, and of many other plants, behave in the same way. Repeated observations have also shown that the petals of Hyacinths and of many Anemones, and the flowers of the Centaury (*Erythræa*), as well as the hollow, honeyless spurs of our

meadow Orchids (*Orchis mascula, militaris, Morio,* &c.), are pierced and sucked by insects, and it should be noted here that not only flies, bees, and humble-bees, but even butterflies are capable of boring into juicy tissue. Butterflies have at the end of their maxillary laminæ which compose their proboscis, certain sharp-pointed appendages with which they first rip up the juicy tissue and then steal the liquid.

A special allurement to those insects which are accustomed to pierce and suck juicy tissues is observed in species of *Eremurus* (*E. altaicus, caucasicus, tauricus*), indigenous in Altai, Caucasus, and Taurus. These plants, which belong to the Liliaceæ, bear a raceme on a long rachis which elongates greatly during flowering. When the flower-buds open the petals are spread out flat, and surround the still closed anthers like a six-rayed star. This only lasts for a short time. As soon as the anthers dehisce and expose their sticky, orange-coloured pollen, the petals roll themselves up, become shrivelled, and form a small dirty red-brown ball, from which spring six thick greenish swellings. These swellings, which are really the juicy veins of the under sides of the petals, resemble green aphides. The fly *Syrphus pirastri*, which is known to seek for Aphides, pierces and sucks these swellings, apparently mistaking them for the insects; at any rate they pierce the rolled-up flowers of *Eremurus* just like Aphides, and, what is most wonderful about the matter, they load themselves by this means with the pollen of the anthers standing in front of the flower, and convey it to the stigmas of other flowers.

We shall have to speak presently of plants whose flowers are only open for a day, a night, sometimes only a few hours. The petals of these plants have this peculiarity, that when they wither they fall quickly, become discoloured, crumpled or rolled up, and pulpy. Then the cell-sap exudes from the tissue and covers the surface with a thin layer of fluid. Pulpy petals of this kind are visited by insects, specially by flies, which lick up and suck the juice, and at the same time cover the stigma with pollen brought from other flowers. This is the case, for example, in *Calandrinia, Tradescantia,* and *Villarsia.* This proceeding is an uncommon one, for the simple reason that the number of plants with such short-lived flowers is very limited.

On the other hand, the secretion of juices on the surfaces of fresh tissues of flowers that remain open several days is a widely-spread phenomenon, so that it is perhaps not too much to say that this secretion occurs in 90 per cent of flowers visited by insects and humming-birds. The secreted juice contains more or less sugar and has a sweet taste. But along with the sugar there are also various other ingredients in solution. According to the variable contents of these ingredients the consistency, the colour, and the smell of the liquid of course vary considerably. Sometimes it is watery and colourless, while at other times it is a thick fluid and brown like treacle. The dark liquid, as it is found in the flowers of *Melianthus,* has an unpleasant and even an offensive odour. But in most cases the smell is similar to that of bees' honey. For the most part this sweet sap is practically the same as honey, and this name is therefore now given to it by most botanists.

Botanists of earlier time called it nectar, and those parts of the flower which prepared and stored it, when they were readily distinguishable, were called nectaries.

The secretion of honey takes place in many cases through stomata, and these are either distributed uniformly over the surface of the tissue, or collected together in particular spots. Usually the stomata are large and of the form known as water-pores. In the Willows (*Salix*) the peg-like or tabular nectary bears only a single large water-pore at its truncated end, which pours out colourless honey. There are also nectaries which are quite devoid of stomata and in which the sweet juice comes to light by diffusion through the outer walls of the superficial cells. Sometimes the inner layer of this cell-wall seems to break down into mucilage, becomes changed into a gummy substance, then into sugar, finally pouring out from clefts in the cuticle which has been raised up like a bladder and burst.

The amount of the honey secreted varies very much. In many plants the drops exuding from the stomata of the petals are so small as to be scarcely visible to the naked eye. In others the honey forms an extremely thin layer, looking as if the tissue had been stroked over with a moist brush. In most cases the small drops flow together into larger drops, which fill the grooves, cylinders, depressions, and cups prepared for their reception. Sometimes these receptacles become filled to overflowing, and then at the least touch the sweet juice flows out of the flowers in drops. This occurs, for example, in *Melianthus major*, growing at the Cape, from whose flowers, with their large cowl-shaped honey-receptacles, an actual rain of honey pours when the inflorescence is shaken. So much fluid honey is secreted by two small horn-like processes in the flower of a tropical Orchid named *Coryanthes*, that it continues to flow for a long time from the points of the horns. The lower end of the so-called lip is hollowed out, and gradually the cavity is quite filled by the trickling honey. The quantity of sweet fluid which so collects amounts to about 30 grammes.

In most instances the most important ingredient of the honey for alluring insects, viz. sugar, is in solution, both on account of its chemical properties and also because the sweet fluid in the hidden grooves and tubes of a flower is thus less exposed to evaporation. Sugar crystals of considerable size formed from the sweet juices of the flower are only found in some Orchids of the genus *Aerides*. It is not necessary to do more than allude to the fact that, as well as in flowers, the sugary solution which pours out from the bracts of certain Composites becomes changed into crumbly crystalline masses, though it may be deserving of short notice. Of this form of sugar as a much-desired food of ants we shall speak in a subsequent chapter.

Usually the honey remains exactly where it has been formed and excreted, but there are some flowers in which this is not so; *i.e.* those where the sweet juice flows from its place of origin and is stored up in special receptacles or honey-bags. This, for example, is the case in the flowers of *Coryanthes*, *Melianthus*, *Viola*, and *Linaria*. It has already been mentioned that in *Coryanthes* there exists an actual collecting-cup, which receives all the honey as it trickles

down from the horn-shaped secreting bodies. In *Melianthus* there are two narrow petals from which the honey drops into the cup-shaped sepal. In *Viola* each of the two lower stamens is furnished with a long process which projects from the connective, and these processes excrete honey, which trickles down into the expansion of the lower, middle petal surrounding them. In the Toad-flax (*Linaria*) the honey is excreted by a cushion at the base of the ovary, but flows from it through a narrow cleft between the two longer stamens into the hollow spur of the corolla directed downwards and backwards.

In addition to portions of the flower proper, bracts can secrete honey. In many flowers single members only are changed into nectaries, but in others a whole whorl of members. Tissue-bodies are often seen which are difficult to explain from the standpoint of speculative morphology, because of the incomplete knowledge of their development, and of which it is impossible to say whether they have arisen directly from the receptacle or from a leaf-structure. On this account it is also not easy to classify or enumerate nectaries in a thoroughly satisfactory manner. If, therefore, in the following a certain order is observed, this is only for the sake of distinctness, and not with the idea that the structures placed side by side belong necessarily to one and the same morphological category.

Fig. 245.—Honey-secreting tissue in flowers.

[1] Flower of the Spindle-tree (*Euonymus europæus*); ×4. [2] Flower of the Red Currant (*Ribes rubrum*) cut through longitudinally; ×5.

In the flowers of most Umbelliferous Plants, of the Cornel, Ivy, Golden Saxifrage, of numerous species of Saxifrage and Spindle-tree (e.g. *Euonymus europæus*, *cf.* fig. 245[1]), a cushion of tissue is developed on the ovary. The stamens and floral-leaves stand round this cushion in a circle but not so as to conceal it, and in the open flower within the corolla the honey may be seen glittering in the sunshine like a thin coat of varnish. The middle of the shallow, basin-shaped flowers of the Sumach (*Rhus*), of the Buckthorn (*Rhamnus*), and of the Red Currant (*Ribes*, *cf.* fig. 245[2]) is covered with a fleshy disc which secretes fluid honey over its whole surface. The Box (*Buxus*) exhibits in the middle of both its staminate and pistillate flowers three little swellings meeting together, each of which deposits a drop of honey. In the Lady's Mantle (*Alchemilla*), *Sibbaldia*, and *Scleranthus* the flower is divided into two stories, into a lower cup-shaped, in which stands the ovary, and an upper, shallower one formed by the floral-leaves. Between the stories is a disc perforated in the middle, or rather a flat ring is interposed which may be compared to the diaphragm in the tube of a microscope. This band also glistens on its upper side in consequence of an extremely thin layer of honey spread over it. The honey-secreting tissue of the Spurge (*Euphorbia*) is very peculiar. The thickly-crowded flowers are surrounded by a cup-shaped envelope

whose edge is studded with crescent-shaped, oval, or rounded bodies. These bodies glisten on their upper side with a thin coating of nectar, just like the cushions on the ovaries of Umbelliferous Plants or of the Spindle-tree.

In the flowers of the Sloe, Almond, and Peach trees, Raspberries and Strawberries, some Cinquefoils, and numerous other Rosaceæ, a fleshy tissue is formed around the ovary or its summit, which, spreading from the base of the flower, lines the calyx-tube like a vestment (*cf.* fig. 246[1]). This tissue secretes honey which, however, is not visible from the exterior, because of the very numerous stamens

Fig. 246.—Nectaries.

[1] Flower of Cinquefoil (*Potentilla micrantha*), the front part cut away. [2] Flower of *Mamillaria glochidiata*, the front part cut away. [3] Flower of *Atragene alpina*, the front part cut away. [4] Stamen of the Atragene with trough-like filament (anther downwards). [5] Four imbricating trough-like stamens of the same plant held together by a spoon-shaped petal. [6] Flower of *Ranunculus glacialis*, the front part cut away. [7] A single petal of the same, seen from above. [8] The petal cut through longitudinally, seen from the side. [3], [6], [7], [8] natural size; the other figs. somewhat enlarged.

which surround it and roof it over. In the flowers of Cactuses, also, the lowest cup-shaped or tubular portion is covered inside with a honey-secreting layer of tissue (*cf.* fig. 246[2] showing *Mammillaria*).

In the Thymelaceæ, Scrophulariaceæ, Gesneraceæ, Boraginaceæ, and Labiatæ the honey-tissue forms a wall surrounding the base of the ovary like a ring; while in the closely-allied Rhinanthaceæ, particularly in the genera *Bartsia*, *Clandestina*, *Lathræa*, and *Pedicularis*, there is a cushion which is attached to only one side of the base of the ovary, and in *Rhinanthus* and *Melampyrum* at the same point a fleshy, honey-secreting lobe. Moreover, in the Cruciferæ, the tissue surrounding the stalk of the ovary is thickened and swollen, while warts and pegs which secrete honey project from it here and there. In the Stocks (*Matthiola annua* and

incana), in *Alyssum*, *Schiverekia*, and *Thlaspi* such warts are seen right and left of the two short stamens, and in *Alliaria* and *Draba* one wart projects from the longer pair of stamens from the outer side facing the corolla. It must remain uncertain whether these structures are to be regarded as part of the stem or as metamorphosed leaves. In many cases—as, for example, in *Haberlea*, *Pœderota*, and *Polemonium*, where the ring-shaped cushion is divided into five, and in *Scrophularia*, where it is divided into two symmetrically-placed lobes—the appearance is in favour of the latter view. In the flowers of the Bindweeds (Convolvulaceæ) the base of the ovary is surrounded by five thick honey-secreting scales of equal size, which together form a small cup reminding one of an egg in an egg-cup, and in the Crassulaceæ a little knob or a fleshy scale projects from the circular wall of the base of the flower opposite each carpel, sometimes spoon-shaped (*Sedum annuum*), sometimes linear and split at the free end (*Sedum atratum*), and of other varied forms. In these instances the honey-secreting structures are without doubt to be regarded as metamorphosed leaves.

Instances are comparatively rare where the formation of honey is carried on by the carpels—as, for example, the flowers of several Primulaceæ (*Androsace*, *Aretia*), in which the slightly arched roof of the ovary secretes minute drops of nectar, and in those of many Gentians (*Gentiana acaulis*, *asclepiadea*, *Bavarica*, *Pneumonanthe*, *prostrata*, *punctata*, &c.), where the bulb-like, thickened base of the ovary exhibits five cushions which exude abundant honey into the base of the flower-tube. In the flowers of some Liliaceæ and Melanthaceæ (e.g. *Albuca*, *Ornithogalum*, *Tofieldia*), the honey is secreted in the lateral grooves of the ovary, and in the flowers of *Anthericum* as well as of *Allium Chamæmoly* a small depression is found on each of the three lines of union of the carpels from which a drop of honey is poured.

Nectaries are found much more frequently on the stamens. They occur there in all sizes and shapes. Sometimes it happens that whole stamens are changed into nectaries, which of course can only be at the expense of the anthers. The stamens of the Whortleberry and Bog-whortleberry (*Vaccinium Myrtillus* and *uliginosum*), like those of Tulips (*Tulipa*), have a small depression which secretes honey on the broad thickened base of the filament opposite the corolla. In the widely-distributed Meadow Saffron (*Colchicum autumnale*) there is an orange-coloured honey-secreting body on the stamens just above the place of union with the violet leaves of the perianth, and the honey there formed fills a channel which traverses the adjoining perianth-leaf. The same thing occurs in other Saffrons and also in the genus *Trillium*. In Geraniaceous plants, especially in *Erodium* and *Geranium*, a wart-shaped, sometimes hollow, nectary arises on the base of each of the five inner stamen-filaments on the side directed towards the sepals. The nectaries at the base of the thread-like filaments of many Caryophyllaceæ exhibit an immense variety of form. Sometimes all the stamens of a flower are a little thickened at their root, and secrete honey from a yellow tissue opposite the ovary (*e.g.* in *Telephium Imperati*), or a pair of honey-secreting

warts are found at the base of each filament (*e.g.* in *Alsine mucronata* and *verna*). Sometimes again only the stamens opposite the calyx have swollen bases which secrete honey on the grooved side opposite the ovary (e.g. *Cherleria sedoides*). In the flowers of *Sagina Linnœi* each of the thread-like stamen-filaments opposite the calyx is surrounded at the base by a cup-shaped nectary. Very often the nectaries of adjacent stamens, in the flowers of the above-mentioned plants, fuse together into a ring, the fusion being only just indicated in the Geraniaceæ, but more decidedly in many Caryophyllaceæ (*e.g.* in *Spergula*), and still more amongst Linaceous and Caryophyllaceous plants (*Linum, Gypsophila, Dianthus, Lychnis*). In the flowers of most Papilionaceæ the stamens form the nectar. Nine stamens are fused into a tube in which the ovary is inclosed. This ovary is at the base of the flower narrowed into a stalk, while the tube, on the other hand, is somewhat widened. Thus is formed a cavity into which honey is poured from the adjacent part of the staminal tube. The space is covered over by the tenth stamen, which, however, yields no honey. In *Atragene alpina*, belonging to the Ranunculaceæ, the abundant honey so eagerly sought by humble-bees is formed in the deeply-grooved inner side of the stamens (*cf.* figs. 246 [3, 4, 5]).

Fig. 247.—Flower of the Snowdrop (*Galanthus nivalis*).

Very often nectar is secreted by the floral-leaves, both in flowers where they form a perianth and also in those where they may be divided into calyx and corolla (*cf.* vol. i. p. 641). In the Snowdrop (*Galanthus nivalis*, see fig. 247), the honey is formed in parallel longitudinal grooves on the inner side of the three outspread perianth-leaves; in Lilies, especially those with hanging flowers and curled perianth-leaves, e.g. *Lilium Chalcedonicum* and *Carniolicum* and the well-known Martagon Lily (*Lilium Martagon*), each perianth-leaf is traversed by a channel studded with bands or ramifying swellings, and filled to overflowing with the abundant nectar secreted in it. Several Orchids, especially species of Twayblade (*Listera*), also exhibit such a channel swollen with sweet sap, but only on one of the perianth-leaves, the lip, which is at the same time the resting-place for the honey-seeking insects while they clear out the channel. In the perianth of the Helleborine (*Epipactis*) the lip is deeply grooved, and resembles a boat filled with honey. In *Epipogium* the perianth-leaf corresponding to the lip is arched like a helmet or cap, and covers the abundant honey there produced. In many other Orchids the lower lip of the perianth is produced backwards, and in the expansion (called the *spur* in descriptive Botany) a quantity of honey is usually hidden. The perianth of *Tricyrtes pilosa* (*cf.* fig. 251 [4]) is composed of six leaves, of which the three outer are expanded near their base and secrete abundant nectar. In the flowers of the *Narcissus* (fig. 248), *Gladiolus*, and *Iris*, also in those of *Sisyrinchium* and *Thesium*, the inner side of the tubular perianth is transformed either wholly, or, at any rate, in the lower third into a honey-secreting tissue

without the development of any special expansion. The nectaries are unusually well-developed on the perianth of the American *Uvularia grandiflora*, in the numerous species of *Fritillaria*, and especially in the Crown-Imperial, often cultivated in gardens under the name of *Fritillaria imperialis*. Each of the six perianth-leaves in these plants exhibits on the inner side near the thickened base a circular, sharply-defined depression in which sparkles a large drop of honey.

Honey is seldom secreted by the calyx. The best examples are the coloured, expanded and fleshy calyx of the various species of the genus *Cuphea* and of the Nasturtium (*Tropæolum*). The species of the last-named genus have a calyx from whose upper portion a long spur projects. Honey is secreted in the narrowed lower portion of this spur, and indeed so abundantly that it sometimes reaches to the mouth.

Fig. 248.—Narcissus (*Narcissus Pseudonarcissus*). [1] The complete flower. [2] The flower cut longitudinally.

And now we come finally to the nectaries in the region of the corolla. Those developed at the base of the flower as well as on the carpels, stamens, perianth-leaves, and calyx, though strikingly varied, are poor in comparison with the wealth of forms which are shown in the petals. In this book it is impossible to give an exhaustive description of these structures, and it must suffice to group together generally the most striking forms and those best fitted to illustrate the processes hereafter to be described. In the corollas of the Mulleins, especially in those of *Verbascum Blattaria* and *phœniceum*, the secretion of honey takes place on the large, lower petal in the form of numerous drops scattered over the middle of the leaf. Each drop comes from a stomate, and, therefore, when the flower opens this leaf looks as if it were studded with dew. But this seldom happens. More usually the small drops flow together, and then a large drop appears in some special spot. In the twining Honeysuckles (*Lonicera Caprifolium, etrusca, grata, implexa, Periclymenum*, &c.), in the Bearberries (*Arctostaphylos alpina* and *Uva-ursi*), in *Allionia* and *Crucianella*, in a species of Winter-green (*Pyrola secunda*), as well as in numerous other plants, honey is secreted in the manner just described in the lowest part of the tubular or bell-shaped corolla. In the Alpine Roses (*Rhododen-*

dron ferrugineum and *hirsutum*), as well as in *Monotropa*, the honey-secreting portion of the corolla is thickened and fleshy, and each of the petals, which are fused together, is hollowed into a groove at the base. In the rotate corollas of *Ophelia*, belonging to the Gentian family, each of the petals is provided with a nectar-depression at its base. In the flowers of the non-twining Honeysuckles (*Lonicera alpigena, nigra, Xylosteum*, &c.) the corolla possesses a honey-forming expansion above the base, and in the flowers of the Calceolarias (*Calceolaria amplexicaulis, floribunda, Pavonii*, &c.) the nectary is hidden in the end of the up-turned lower petal as if in a shell. The corolla of the Valerian (*Valeriana globulariæfolia, montana, officinalis*, &c.) manufactures its honey in a small expansion which may be seen on the side of the corolla-tube (*cf.* fig. 249), and in the flowers of the Butterwort (*Pinguicula*) the corolla is narrowed backwards into a pointed spur just about equalling it in length. In the flowers of the Pansy (*Viola*), only one of the five petals has a honey-collecting spur; in those of the Columbine (*Aquilegia*), on the other hand, each of the petals is drawn out into a spur which develops honey in its club-shaped, thickened end. The small white petals of the Sundew (*Drosera*) terminate at their base in a yellow claw whose tissue secretes a little honey. The same thing occurs in the flowers of the Buttercup (*Ranunculus*), only here the honey-producing tissue is sharply defined and appears as the lining of a circular or oval depression, which, in many cases, is uncovered—as, for example, in *Ranunculus alpestris*—but in others is roofed in by a scale, as in *Ranunculus glacialis* (see figs. 246[6, 7, 8]). The flowers of *Hypecoum* have two opposite petals, each divided into three lobes, and at the base of these, under the central lobe, a large pit is developed which is filled with the honey abundantly secreted there (see figs. 251[5] and 251[6]). The nectaries in the flowers of *Swertia*, belonging to the Gentianaceæ, are very remarkable. Two pits surrounded by a strong circular wall are seen some millimetres above the base of the flower on each petal, and a long fringe like a portcullis hangs down from this wall over the pit. The tissue which forms the lining of the pit develops a quantity of honey, and as the grating does not completely cover the pit the honey may be seen shining through it.

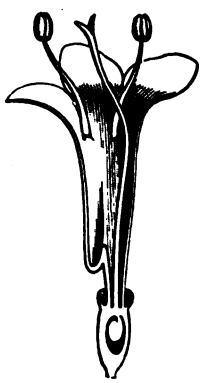

Fig. 249.—Flower of the Wild Valerian (*Valeriana officinalis*), cut through longitudinally.

We must also consider here those remarkable nectaries interpolated between the floral-leaves and stamens of many Droseraceæ, Berberidaceæ, and Ranunculaceæ, to which the name of "honey-leaves" has recently been given. They display the most peculiar forms, and correspond but slightly to the description commonly given of a leaf. For example, in the Grass of Parnassus (*Parnassia*, fig. 267[5]), belonging to the Droseraceæ, they resemble a hand, on the concave side of which are two honey-secreting depressions, the eleven slender processes which correspond to the fingers terminating in rounded heads. In the flowers of *Epimedium*, belonging to the Berberidaceæ, they are shaped like a slipper. In those of Love-in-a-mist

(*Nigella*), of the Ranunculaceæ, they resemble a covered bowl with a stem, or a hanging lamp (see figs. 250[4, 5, 6, 7]). In the flowers of the Monkshood (*Aconitum*), they take the shape sometimes of a Phrygian cap, sometimes of a cowl, and occasionally of a French horn, and are carried by a long, erect stalk traversed by a channel. In the flowers of the *Isopyrum* as well as in those of *Cimicifuga*, they resemble shovels or spoons, which carry two puzzling knobbed processes at their free ends. The flowers of the Winter Aconite (*Eranthis*), and of the Christmas Rose (*Helleborus*), exhibit nectaries of a trumpet, cup, or tubular form with obliquely-truncated mouth within the large calyx, and those of the Globe-flower (*Trollius*) conceal numerous spatulate nectaries, which are somewhat bent and thickened in the lower third, where they are provided with a honey-secreting pit (see fig. 221[3], p. 110). In the flowers of the Pasque-flower (*Pulsatilla vernalis* and *vulgaris*), between the large, flat floral-leaves, and the anther-bearing stamens, small club-shaped structures are interpolated in two or three spiral series. These secrete abundant honey which moistens the base of the neighbouring stamens. All these honey-leaves may be regarded either as modifications of petals or of stamens. Those of *Epimedium*, Love-in-a-mist, Monkshood, and *Isopyrum*, remind one more of the former, those of the Globe-flower and Pasque-flower of the latter. The opinion was stated in vol. i. p. 646, that all perianth-leaves might be metamorphosed stamens, consequently it is idle to inquire whether the honey-leaves are to be regarded as petals or as stamens.

From the point of view of the visits of animals these questions as well as others of speculative morphology are unimportant. But, on the other hand, it is of importance to group together into two divisions those nectaries which we have hitherto but cursorily noticed from a morphological aspect. One of these divisions will comprise the nectaries whose sweet fluid is exposed to the daylight, the other those in which the honey is concealed in hidden nooks at the base of the flower.

The exposed honey is accessible to all flower-visiting animals, but can be appropriated with good results only by some of them. The varnish-like coating of honey, for example, which is spread over the cushion of tissue on the ovary of the Spindle-tree, Ivy and Cornel, Saxifrages and Umbelliferous plants cannot be sucked up by butterflies and humble-bees with long probosces. But it is just this honey which is the centre of attraction for beetles, flies, gnats, and other insects with short probosces. On the flowers of the plants named there are actually swarms of beetles of the genera *Anthrenus*, *Dasytes*, *Meligethes*, *Telephorus* and *Trichius*, as well as innumerable flies and gnats which lick up the thin layer of honey with their tongues or their flatly-extended probosces. And the honey which is displayed in the form of large drops in the depths of the lip of the flowers of the Helleborine (*Epipactis*), and in the corolla of the Figwort (*Scrophularia*) is sought for only by insects with short probosces, particularly by wasps, while it is avoided by humble-bees and butterflies.

With the honey hidden in concealed pits, tubes, and channels, exactly the opposite occurs. This is inaccessible to most of the insects with short probosces

but forms the principal food of humming-birds, butterflies, humble-bees, &c. Of course there is again the utmost variety according to the length of the proboscis or bill, and the depth of the hiding-places in which the honey is concealed. The distance of the honey-secreting base from the restricted mouth of the corolla amounts in the flowers of the Heath (*Erica carnea*) to only a few millimetres, while it reaches 16 centimetres in those of the Rubiaceous *Oxyanthus tubiflorus*, which grows in Sierra Leone. In *Angræcum sesquipedale*, a species of Orchid growing in Madagascar and distinguished by the size and splendour of the

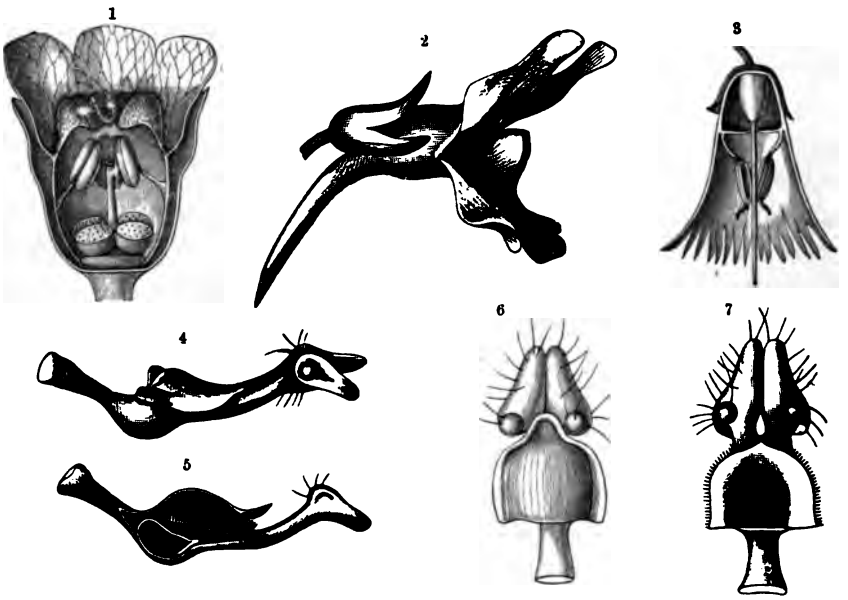

Fig. 250.—Concealment of Honey.

[1] Flower of *Cynoglossum pictum*, the front part of the flower cut away. [2] Flower of *Linaria alpina*. [3] Flower of *Soldanella alpina*, the front part of the flower cut away. [4] A honey-leaf of *Nigella elata*. [5] The same cut through longitudinally. [6] A honey-leaf of *Nigella sativa*, seen from above. [7] The same; the roof covering the nectar-pit cut away. All the figures somewhat enlarged.

inflorescence, the perianth possesses a hollow spur 30 centimetres long which is filled with honey at its base.

There are two kinds of contrivances for hiding the honey in pits, tubes, and channels. In the one the entrance to the hiding-place is narrowed by all kinds of inflations, cushions, bands, and flaps at the mouth of the flower-tube (see fig. 250[1] of the flower of *Cynoglossum*). In the other the nectary is completely closed over by a roof or door, or by two lips, so that those animals which desire the honey stowed away in the cavity are compelled either to raise the roof, to open the door, or to press down one of the lips. As examples of the latter kind of closing may be instanced the flowers of *Corydalis*, of the Fumitory (*Fumaria*), of the Snapdragon (*Antirrhinum*), and of the Toad-flax (*Linaria*; see fig. 250[2]), whilst in some Soldanellas (*Soldanella*; see fig. 250[3]), and in the genus *Aechmea*, belonging to the Bromeliaceæ, the closure is effected by special scales, like folding doors, introduced into the corolla-tube.

Sometimes the stamens are so fashioned and disposed as to form an overarching roof or dome above the honey-secreting base of the flower, *e.g.* in numerous Solanaceæ, Primulaceæ, Boraginaceæ, and Campanulaceæ (*Nicandra, Cyclamen, Borago, Campanula, Phyteuma*); very beautifully also in the Willow-herb (*Epilobium angustifolium*), in *Gladiolus*, and in the small-flowered Cinquefoil (*Potentilla micrantha*) pictured in fig. 246[1]; finally in the Mammillarias, belonging to the Cactaceæ (see fig. 246[2]).

The hiding of the nectaries by a massing together of the stamens is effected in

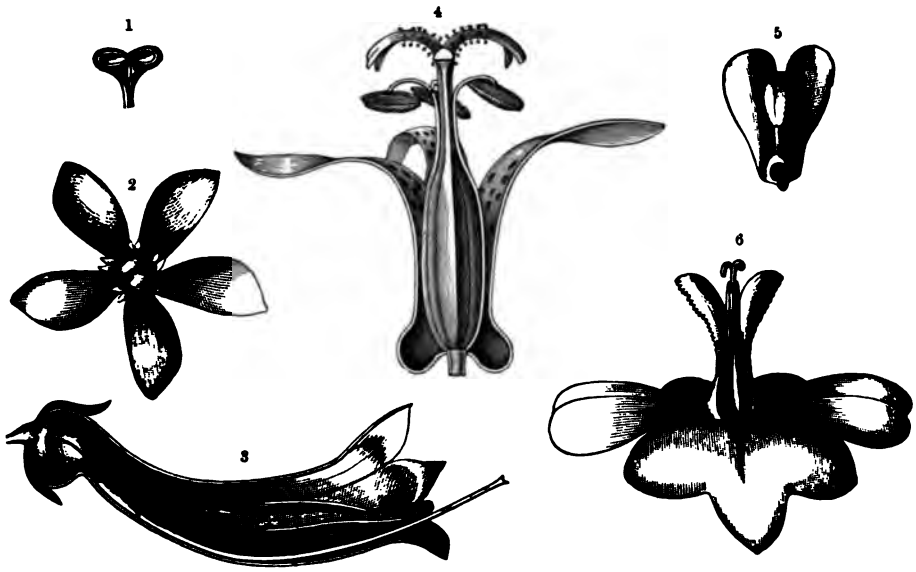

Fig. 251.—Concealment of Honey.

[1] Stigma of *Gentiana Bavarica* which closes the corolla-tube, removed from the flower. [2] Flower of the same plant seen from above. [3] Flower of *Phygelius capensis*; the front half cut away. [4] Flower of *Tricyrtis pilosa*, the anterior part cut away. [5] One of the two inner petals of *Hypecoum grandiflorum* seen from the side adjacent to the ovary. [6] Flower of *Hypecoum grandiflorum* showing the two inner petals standing close to the ovary.

a very strange manner in some white-flowered Crow-foots, *e.g.* in *Ranunculus glacialis*. In these plants the honey is secreted in small pits on the upper side of the petals close above the yellow, thickened claw (see fig. 246[6, 7, 8]). In front of this pit is a scale which rises from the plane of the petal at an angle of 40°–50°. On and near this scale lie the numerous stamens arranged in several whorls radiating out from the centre of the flower. A small nectar-cavity is thus formed at the base of each petal to which only those insects strong enough to press up the overhanging stamens and the scale can gain entrance. In the flowers of the *Atragene alpina* the stamens are hollowed into a groove in which a quantity of honey is secreted (see fig. 246[4]). But as in each flower there are many whorls of stamens—those of the outer whorls always covering and being attached to the backs of the inner ones (see fig. 246[3]), and as all the stamens are held together outside by a whorl of erect, stiff, spoon-shaped leaves (see fig. 246[5])—all these channels form, as it were, many small, closed, nectar-cavities only to be opened by powerful insects.

The flowers of the *Phygelius capensis* (illustrated in fig. 251[3]) show at the base of the tubular corolla a small expansion filled with honey which is converted into a closed cavity by the ovary bending down in front of it and pressing itself closely to the wall of the corolla-tube. In the flowers of *Tricyrtes pilosa* (see fig. 251[4]), whose three outer perianth-leaves secrete honey in the expansion at the base of the flower, the three-sided ovary is wedged in like a prop between the perianth-leaves, and three closed nectaries are thus formed out of the expansion. A similar appearance is also observed in the flowers of *Hypecoum procumbens*. Here the honey is secreted in a pit close above the claw of the two inner petals (see fig. 251[5]). Just as in *Ranunculus glacialis*, so here, this pit is covered by a peculiar scale which is fitted to receive the pollen at a certain stage of development, as will be afterwards described. This scale is erect and parallel to the ovary, its base being in contact with it (*cf.* fig. 251[6]). In this way the pit or nectary is completely closed in.

It may be remarked finally that in many cases the stigma may act as a covering to excavated, honey-containing flowers. This is so, for example, in the Gentians of the group *Cyclostigma*, the flower and stigma of one species of which (*Gentiana Bavarica*) are illustrated in figs. 251[1] and 251[2].

THE COLOURS OF FLOWERS CONSIDERED AS A MEANS OF ATTRACTING ANIMALS.

If we wish that certain distant objects should be plainly seen, it is usual, as is well known, to assist the eye by contrasts of colour. We place signals on the railways with a red band on a white background, put gold letters on black sign-boards, and paint a black circle and a black spot on the white disc towards which we point the gun. The same colour-contrasts occur in plants whose flowers are the aim of flying animals.

Since flowers in most cases open above green foliage-leaves, it is evident why in the floral region those colours are most often met with as allurements which contrast well with green. Of those plants of the Baltic flora whose flowers are displayed against a background of green, 33 per cent are white, 28 per cent yellow, 20 per cent red, 9 per cent blue, 8 per cent violet, and 2 per cent brown. Looked at from a distance white, yellow, and red stand out best from the green of the foliage, blue and violet only a little, and brown scarcely at all.

Usually it is the petals whose colour standing out from the surroundings makes the flowers conspicuous from a distance. That side which is presented towards the flying insects displays the colour most brightly. When the corollas or perianths are pitcher-shaped or bell-shaped, nodding or pendulous, so that the animals on approaching do not see into the inside of the flower, the outside is coloured the more brilliantly. But if, on the other hand, the flower is star-shaped or disc-like, with its face turned to the sky, and to the swarming insects, then the inner side shows the brighter colours. There are even some flowers whose petals are

coloured yellow, white, or red on the inside only, while the outer side is green. Those, for example, of *Gagea* are yellow on the inside only whilst the outside is green. When these flowers are closed they do not strike the eye; only when opened in the sunlight does the yellow star show up from the background. The same thing may be said of the flowers of the Star of Bethlehem (*Ornithogalum*), of the Lesser Celandine (*Ranunculus Ficaria*), of the Pimpernel (*Anagallis*), of the Venus's Looking-glass (*Specularia*) and of many other plants.

In some instances where the petals have been transformed into nectaries, or have assumed some other function, which would not easily allow of their developing brightly-coloured surfaces, the duty of alluring the animals is performed by the sepals. These are then not green, but are coloured white, yellow, red, blue, violet, or brown, as, for instance, those of the Christmas Rose and of the white Wood Anemone (*Helleborus niger, Anemone nemorosa*), of the Globe-flower and Winter Aconite (*Trollius, Eranthis*), of the Atragene and of the Monkshood (*Atragene alpina, Aconitum Napellus*), of the Pasque-flower and of the Marsh Cinquefoil (*Pulsatilla pratensis, Comarum palustre*). And of course the features noted above in the case of the petals is repeated in these flowers—the outer side of the calyx is brightly coloured in the hanging bells of the Marsh Cinquefoil, but the inner side in the star-shaped, open flowers of the Pasque-flower.

Nor do the stamens, in comparison with the corolla, calyx, or perianth, frequently serve as attractive organs to animals in virtue of peculiar colouring. In Northern and Central Europe we notice the Willows—destitute of perianth-leaves—rendered conspicuous from afar by their numerous, crowded stamens with red or yellow anthers. In other cases the flowers are conspicuous in virtue of their brightly-coloured stamen-filaments—white, purple, red, or yellow—as in certain Ranunculaceæ, e.g. *Actæa, Cimicifuga*, and *Thalictrum*, still more in the Acacias of Australia, and in the genera *Callistemon* and *Metrosideros* belonging to the Myrtaceæ, in the Japanese *Bocconia*, as well as in several species of *Æsculus* (e.g. *Æ. macrostachya*). The flower-spikes of the North American *Pachysandra*, which trail along the ground, yet stand out from the dark environment because the filaments are dazzling white. In several Asiatic Steppe-plants, viz. in species of *Halimocnemis* (see figs. 252[10] and 252[11]), a bladder-like appendage rises above each anther, and is coloured sulphur-yellow, violet, bright or dark red, and thus stands out brilliantly from the gray-green surroundings and might easily be mistaken at first sight for a petal.

It often happens that the bracts which subtend and enfold the flowers rather than the flowers themselves attract attention by the contrast of their colours with the surrounding green. Numerous examples are furnished by the Cornel (e.g. *Cornus florida* and *Suecica*; see fig. 252[12]), the Myrtaceæ (*Genetyllis tulipifera*), the Umbelliferæ (*Astrantia, Bupleurum, Smyrnium, Eryngium alpinum*), the Labiatæ (*Nepeta reticulata, Salvia splendens*), Compositæ (*Cirsium spinosissimum, Gnaphalium Leontopodium, Xeranthemum annuum, Carlina acaulis*; see p. 117), the Spurges (*Euphorbia polychroma, splendens, variegata*), the Aroids

(*Richardia æthiopica, Anthurium Scherzerianum*), and the Bromeliaceæ (*Nidularia, Lamprococcus, Pitcairnia*). In some Proteaceæ, e.g. *Protea globosa*, the uppermost foliage-leaves are grouped into a large outer envelope which surrounds the spherical golden-yellow inflorescence, and these crowded leaves are coloured

Fig. 252.—Colour-contrasts in Flowers.

[1] Umbellate raceme of *Lobularia nummulariæfolia* with flowers and young fruits. [2] A single young flower of the same plant. [3] A young fruit of the same plant with two of the enlarged white petals attached to it. [4] Flower spike of *Lavandula Stœchas* ending in a crest of empty blue bracts. [5] Umbellate raceme of *Alyssum cuneatum* with young flat open flowers in the centre and old closed flowers at the circumference. [6] Petal of a young flatly-opened flower of the same plant. [7] Petal of an old closed flower of the same plant. [8] Raceme of *Muscari comosum*; the upper long-stalked flowers crowded into a head are sterile. [9] Inflorescence of *Trifolium badium*; the upper young flowers are light yellow, the old lower drooping flowers are dark brown. [10] A branch from the inflorescence of *Halimocnemis mollissima*; the erect bladder-like appendages of the anthers protrude from the insignificant perianth and look like petals. [11] A single stamen of *Halimocnemis mollissima*; the connective rises above the anther in the form of a bladder-shaped appendage. [12] Inflorescence of *Cornus florida* surrounded by four large white bracts. [13] Cornflower (*Centaurea Cyanus*); the small flowers of the disc are surrounded by large funnel-shaped sterile flowers. [14] Raceme of *Kernera saxatilis*; the ovaries in the centre of the old flowers are darkly coloured and surrounded by the enlarged petals. [15] Inflorescence of the umbelliferous *Orlaya grandiflora*; the peripheral flowers radiate outwards. [16] A single radiating flower of the same plant. [17] Umbellate raceme of the Candytuft (*Iberis amara*); the outwardly-directed petals of the peripheral flowers are twice as large as those which are turned towards the centre of the inflorescence. 2, 6, 11 are somewhat magnified; the others natural size.

blue in contrast to the lower, scantier foliage, which has a grass-green colour, in order that the inflorescence should stand out the better. Even the stalks of flowers and inflorescences when brilliantly coloured may be seen from a distance and so

furnish a means of allurement, as is the case in *Eryngium amethystinum, creticum*, &c., as well as other plants.

When a coloured object is less than a certain size not even the most vivid red, the brightest yellow, or most dazzling white will render it visible at a distance. If the parts of the flower or the envelopes whose function is to attract flying animals from a distance are to be serviceable as signs, they must occupy a considerable space, a necessity provided for in various ways, one of which is the large size of the individual flower. But it would be an error to suppose that this method, from its apparent simplicity, is the most frequent; in point of fact it seldom occurs. Scarcely one in a thousand of the flowers of Phanerogams exceeds 10 centimetres in diameter, and most of these are found only in tropical countries. A species of *Rafflesia*, which has the largest flowers in the world, is illustrated in vol. i. p. 203. The *Rafflesia Schadenbergiana*, which flourishes in the Island of Mindanao in the Philippines at a height of 800 metres above the sea, parasitic on the roots of *Cissus* plants, develops flowers weighing about 11 kilograms a-piece, with a diameter of about 80 centimetres. To be mentioned with these Rafflesias, in respect of extreme diameter, are the flowers of the rare Peruvian orchid, *Paphiopedilium* (*Cypripedium*) *caudatum*, whose ribbon-like lateral petals attain a length of 70 cm. These tailed lateral petals hang down moustache-like right and left of the flower, and though when the flower first expands they are only some 10 cm. long, they continue growing for about ten days, in which time they usually attain their full length. From the second to the seventh day they have been observed to increase in length as much as 5 cm. each day. Very large also are the balloon-like flowers of several tropical American Aristolochias, of which it is stated that children use them in play as caps and pull them down over their heads. Thus the flowers of the Guatemalan *Aristolochia gigas*, var. *Sturtevantii* (cultivated in the Botanic Gardens at Kew) are about 45 cm. wide, 55 cm. long, with a tail exceeding a metre in length; their colour is creamy yellow and deep maroon purple. But of course the amount of substance composing these tailed and inflated flowers is as nothing compared with that which goes to make a huge *Rafflesia*-flower. The flowers of *Magnolia Campbellii* belonging to Sikkim (Himalaya) display almost as great a diameter as those of these tropical creepers. When the erect red flowers of this tree open in the sunshine they show a width of 26 cm., a size never attained by any other tree-flower. One of the Lotus plants, viz. *Nelumbo speciosum*, as well as the Australian *Nymphæa gigantea*, produces flowers with a diameter of 25 cm.; the *Lilium auratum*, recently much planted in European gardens, flowers of 24 cm. Many Cactuses exhibit flowers with a diameter of 20–22 cm., viz., *Echinopsis cristata, Cereus grandiflorus*, the Queen of the Night (*Cereus nycticalus*), besides the following from other groups, the South American *Datura Knightii, Nymphæa Devoniensis*, and the celebrated *Victoria regia* of the River Amazon, all of these possess flowers of colossal proportions. *Nelumbo luteum, Amaryllis solandriflora*, and the Opium Poppy (*Papaver somniferum*) have flowers of 16–18 cm. diameter, *Amaryllis aulica* and *equestris, Datura ceratocaula* and *Pæonia*

Moutan of 13–15 cm., several Mexican Cactuses (e.g. *Echinocactus oxygonus* and *Tetani*) and the Gourd (*Cucurbita Pepo*) flowers of 10–12 cm. diameter.

Another method by which flowers are rendered conspicuous to the naked eye is the massing together in bunches, spikes, racemes, umbels, and capitula. A single flower of the Elder (*Sambucus nigra*), with a diameter of only 5–6 mm., would be scarcely visible on its dark background at a distance of 10 paces, while a thousand or fifteen hundred of such flowers arranged in a flat nosegay of 16–18 cm. diameter show up quite plainly at the same distance from the dark-green foliage. Even the flowers of the American weed, *Galinsoga parviflora*, recently established in Europe, which are amongst the smallest in the world, having only a length of 1 mm. and diameter of 0·3 mm., become so conspicuous when crowded together in great numbers on a flat disc that they may be easily distinguished by the eye at a distance of 15 paces. The flowers of about 10,000 different Composites, 1300 Umbelliferæ, and innumerable Valerians, Pinks, Stitchworts, Spiræas, Papilionaceæ, and Labiatæ are only visible at a distance because crowded together. If isolated their minuteness would prevent them from being noticed.

Very often it is only a part of the flowers which, when collected into umbels, racemes, and capitula, make the whole conspicuous. In species of *Iberis* belonging to the Cruciferæ (e.g. *Iberis amara, gibraltarica, umbellata*; *cf.* fig. 252[17]), in most Scabiouses (e.g. *Scabiosa Columbaria, cretica, graminifolia*), and in not a few Umbelliferæ (*Daucus, Heracleum, Orlaya*; *cf.* figs. 252[15] and 252[16]), the flowers growing at the circumference of the umbel or capitulum show an enlargement on one side; *i.e.* those petals which are turned away from the centre of the inflorescence are considerably increased and look like short rays proceeding from the periphery. Some Cruciferæ of the genera *Alyssum, Dentaria*, and *Sisymbrium* are also remarkable instances. It cannot be said of these that the flowers standing at the circumference of the umbellate group are really enlarged on one side, yet they have the same appearance as the radiating flowers. This is accounted for by the fact that the petals do not fall off after the deposition of pollen on the stigmas, but remain behind, fold together like the leaves of a book, and, what is still more remarkable, after a little while grow together. When the flowers of *Alyssum montanum, Wulfenianum* and *cuneatum* (*cf.* fig. 252[5]) reach the highest point of their development, when pollen is formed by their anthers, and honey for insects stored in the flower base, the yellow petals have a length of 3–4 mm.; but when once the anthers have given up their pollen and the flower base is cleared of its honey, when the stigma has dried up and the ovary has already grown into a small fruit, then the petals attain a length of 6–7 mm. (*cf.* figs. 252[6] and 252[7]). Thus, while the flowers which have just reached maturity and stand in the centre of the group are small and insignificant, those at the circumference display enlarged petals radiating outwards, thus rendering the whole inflorescence conspicuous. In other words, the older flowers are actually occupied in the allurement of insects for the advantage of the younger ones.

The difference between the peripheral and central flowers of one and the

same head does not always consist only in the enlargement of one side, but in many plants in the actual development of different forms of flower. In these the flowers of the centre stand erect and are tubular, while those of the periphery radiate outwards, are larger, coloured much more brilliantly, and are shaped either as short broad plates as in the Milfoil (*Achillea*), or like long narrow tongues as in *Arnica montana*. In the Cornflower (*Centaurea Cyanus*, *cf.* fig. 252 [13]) and in allied species the peripheral flowers assume the form of funnels with split edges. One seeks in vain for anthers and stigmas inside these flowers; they have become unfruitful and sterile, and in this way a complete division of function has taken place in the two kinds of flowers of the Cornflower capitulum. Here it is only the flowers of the centre which are provided with stamens and pistils, and which conceal honey at the base of their small tubes; these alone are fertile. On the other hand, they are insignificant in appearance, and at a little distance would not be noticed. Thus the sterile, funnel-shaped flowers, visible from a distance on account of their beautiful azure blue, surround their fruitful neighbours, and perform the task of attracting the insects to them. This remarkable division of labour in flowers of one and the same capitulum seen in Cornflowers may be also noticed in many cymose inflorescences—as, for example, in the Guelder-rose (*Viburnum Opulus*) and in Hortensias (*Hydrangœa Japonica, quercifolia*, &c.; *cf.* fig. 222 [8]). Of course only in the wild specimens, for the Guelder-rose grown in gardens, as well as those plants which horticulturists call Hortensias, have inflorescences consisting entirely of sterile flowers from which no fruit can be produced.

While in the last-mentioned plants the sterile flowers which attract insects are found at the circumference of the capitulum or umbel, one meets with a bunch of sterile flowers at the top of the racemose inflorescence in many species of *Muscari*, allied to the Hyacinths (e.g. *Muscari comosum* and *tenuifolium*; *cf.* fig. 252 [8]). These are very remarkable on account of their bright colour, and obviously perform the same function on behalf of the less conspicuous fruitful flowers below as do the sterile flowers in the capitulum of the Cornflower.

When the bracts enveloping the flower heads assume the function of alluring insects, and are consequently coloured white, yellow, red or blue, each of these structures singly is usually of such a small size that it could not be seen even at a very little distance; but their aggregate effect is such that the whole inflorescence is conspicuous from afar. The dry scales surrounding the flower-heads are coloured snow-white, golden-yellow, or rose-red in the species of *Helichrysum* known as Immortelles—for example, in the sacred flower which the Greek pilgrims bring with them from Mount Athos (*Helichrysum virgineum*), in the beautiful *Helichrysum frigidum* of the Corsican uplands, in the yellow-headed *Helichrysum arenarium* growing on the sandy heaths of the Rhine valley, and in the numerous species spread over the rocky heights in the Cape. It is evident that the effect of the scaly, coloured envelopes is materially increased when the flower-heads they surround are massed together in numbers forming dense tufts. It thus happens

that inflorescences whose individual parts only measure a few millimetres may be plainly seen at a distance of many hundred paces. Fig. 253 is an illustration taken from nature of the Haastias (*Haastia pulvinaris* and *Sinclairii*), composites which grow in New Zealand on mountains of 1200 to 2000 metres in height, and are a good example of the above. The innumerable flower-heads of this plant are crowded together into hemispherical masses which reach a height of half a metre with the diameter of a metre. Both the scaly envelopes and the flowers are coloured white, and since these Haastias grow on rocky heights upon a background

Fig. 253.—Two New Zealand Haastias (*Haastia pulvinaris* and *Sinclairii*, the latter species in front) called "vegetable sheep" by the English colonists in New Zealand.

of dark earth and stone they stand out conspicuously from their surroundings. The colonists name these plants "vegetable sheep", often mistaking them, so it is said, for fugitives from their flocks, and take long journeys in order to bring them back, only discovering the true state of the case to their great annoyance when close at hand.

The bracts of many species of Lavender and Sage (*Lavandula pedunculata, Stœchas, Salvia viridis*, &c.), growing in the floral region of the Mediterranean, become sources of allurement in a very strange manner. Those which grow beneath the bunches of flowers on the lower half of the spike are insignificant, but at the top, where the flowers are not developed, the bracts are enlarged, brilliantly coloured, and crowded into tufts, resembling the white or red flowers used as

trophies by builders to celebrate the completion of a certain stage of their work (*cf.* fig. 252[4]).

The plants which have hitherto been selected to illustrate the significance of colour in flowers, whether in the blossoms themselves or in their bracts, exhibit only one tone of colour in contrast with the foliage green; that is to say, the entire flower, the whole inflorescence, or the complete group of bracts appears from a little distance as simply white, yellow, red, violet, or blue, and stands out conspicuously from the environment on account of one of these colours. It often happens, however, that the colour-contrast is obtained by the development of several colours in the flowers. In the blossoms of many Willow-herbs (e.g. *Epilobium hirsutum* and *montanum*), the white cross formed by the stigmas appears on a red field; in the Herb Paris (*Paris quadrifolia*) the bright yellow anthers encircle the large, dark-violet ovaries. In the centre of the flowers of the Borage (*Borago officinalis*) a black cone of anthers rises from a blue star, and a yellow cone of anthers on a violet star in the Bitter-sweet (*Solanum Dulcamara*) and in the Potato. In the flowers of the Pheasant's-eye (*Adonis flammea, æstivalis, autumnalis*), the numerous black anthers form a dark centre on a red ground, and an orange centre on a blue ground in the Jacob's Ladder (*Polemonium cæruleum*), whilst in the flowers of the Hepatica (*Anemone Hepatica*) a white centre is seen on a blue ground, and in the flowers of many Mulleins (*Verbascum austriacum, nigrum*) occur stamens with violet hairs which contrast with the light yellow corolla and orange anthers. The dark violet petals of *Saxifraga biflora* surround a centre of golden-yellow, and in the Ice-plant (*Mesembryanthemum crystallinum*), so common at the Cape, the yellow centre formed by the crowded anthers is surrounded by a large number of narrow, radiating, red petals.

Fig. 254.—Colour-contrast in the flowers of the Bean (*Vicia Faba*). The wings (alæ) of the white papilionaceous corolla are ornamented with large black eye-spots.

In all these instances the stigmas and stamens stand out from the petals, but it may happen that the floral-leaves themselves are thus rendered conspicuous by a contrast of colours, as, for example, in the flowers of *Victoria regia*, whose outer petals are white, and the inner crimson. In Papilionaceous flowers it is often observed that the upwardly curved petal called the standard is coloured differently from the keel and the wings. The Vetches and Peas (*Vicia picta, Lathyrus odoratus, Baptisia australis*) may be quoted as examples. Those Papilionaceous flowers are most remarkable in which the two lateral wings are dark violet or almost black, and look like two dark eyes below the yellow standard (*e.g.* in *Vicia Barbazetæ, Melanops*, and *Faba*; see fig. 254). In thousands of flowers the petals are marked with spots, speckles, stripes, bands, and borders, the contrasting colours being set next one another. The white perianth-leaves of the Snowflake (*Leucojum vernum*; *cf.* fig. 244) have a green spot near the apex; the scarlet-red standard of the butterfly-corolla of *Clianthus Dampieri* carries a dark-violet eye-spot in the centre; the orange tongue-shaped flowers of *Gorteria ringens* have a black spot at the base, in which are scattered white stripes and dots; the delicate perianths of *Sisyrinchium anceps* are blue or violet above, but yellow or orange below. The white coronas of the Narcissus (*Narcissus poeticus*; *cf.* fig. 255) are surrounded by a cinnabar-red border; and in the blue flowers of the Forget-me-not (*Myosotis*), the mouth of the short tube has an irregular yellow ring round it. Those plants which have been called "*tricolor*" on account of the various tints of their flowers, *e.g.* the three-coloured Bindweed (*Convolvulus tricolor*), the Pansy (*Viola tricolor*), and the three-coloured Vetch (*Vicia tricolor*), may also be quoted as examples.

Fig. 255.—Narcissus (*Narcissus poeticus*); the Corona in the centre of the flower is fringed with a cinnabar-red border (black in the figure).

Sometimes the spots, points, and stripes standing up from the ground-colour of the flowers perform the double function of showing the entrance to the honey easiest for the approaching insects, and at the same time most advantageous to the plant itself. Of this we shall speak more particularly later on. But it would be too much to say that all spots are to be regarded as signals or to call them "honey-indicators" or "path-finders". They are found often enough in flowers from which honey is altogether absent, as, for example, in those of *Hibiscus Trionum*, and of the opium and common red Poppies (*Papaver somniferum* and *Rhœas*), where their only use can be to show up the flowers. It should be noted here that

flowers with finely-marked petals are ardently sought for, indeed, almost exclusively, by flies. Many Orchids and Labiate flowers, but especially many Saxifrages (*Saxifraga Aizoon, aizoides, bryoides, rotundifolia, stellaris, sarmentosa*, &c.), are very instructive examples. We cannot, indeed, explain what connection there is between the visits of flies and the yellow, red, or violet dots which in some species sometimes change their colour during the period of flowering. But it is certain that the minute red and yellow spots on the petals of these Saxifrages do not make the flowers more visible or conspicuous to the human eye.

A brilliant contrast is caused by the difference in the colours of the corolla and the adjacent outspread bracts and sepals. The flower of *Acanthus*, whose upper sepal is coloured violet, while the petals below it are white, deserves special notice in this connection. Also those of *Clerodendron sanguineum* with white sepals and blood-red petals, as well as the inflorescence of many species of the Cow-wheat (*Melampyrum arvense, grandiflorum, nemorosum*), whose blossoms are yellow and the bracts blue, violet, or red. Lastly, we may mention *Sideritis montana* and *Romana*, whose small, brown petals project like dark points from the yellow bracts.

In the capitula of Composites whose flowers are crowded closely together, the florets of the ray and of the disc usually display different colours. As examples of this common form of colour-contrast may be mentioned the Ox-eye Daisy (*Leucanthemum vulgare*), whose yellow disc-flowers are surrounded by white ray-flowers; *Pyrethrum carneum*, with yellow disc-flowers and red ray-flowers; Rudbeckias and Zinnias (*Rudbeckia laciniata, fulgens, Zinnia hybrida*, &c.), whose dark-brown disc-flowers are surrounded by yellow ray-flowers, and almost all the numerous series of Asters with yellow disc-flowers and blue ray-florets.

Contrast of colour is also frequently produced by the corollas changing their colour at various stages of development. In the bud they are red, after opening they become violet, and then when they wither they become blue or malachite green. When such flowers are crowded together a very effective colour-contrast may result. Especially remarkable in this respect are the Bitter Vetches (*Orobus vernus* and *Venetus*), and several Boragineous plants belonging to widely different genera (e.g. *Pulmonaria officinalis, Mertensia Sibirica, Symphytum Tauricum*), and also some Willows (e.g. *Salix purpurea, repens, Myrsinites*), in which latter the crowded anthers appear at first purple, red, then yellow, and finally black. The tubular flowers of the flat disc-shaped head of Telekia (*Telekia speciosa*) are yellow at first, but later become brown, and since the flowers open successively from the circumference towards the centre of the head, when the blossom is at its height the yellow centre is surrounded by a dark-brown ring. In many species of Clover (*Trifolium*), the faded corollas do not fall off at the end of the flowering period, but wither and dry up, and envelope the small fruit like a mantle. The stalks of the flowers grouped into umbellate heads then bend downwards and arrange themselves into a wreath surrounding the upper, younger flowers which stand erect and are, of course, of a different colour. Thus in the Bastard Clover (*Trifolium hybridum*), the young, erect, densely-crowded, white flowers are

surrounded below by a garland of older, rose-red flowers; and in *Trifolium spadiceum*, the light-yellow centre formed by the young flowers is surrounded by a zone of chestnut-brown older flowers whereby a very remarkable colour-contrast is brought about (*cf.* fig. 252 [9]).

The contrasts met with in the umbel-like racemes of the small-flowered Cruciferæ are also extremely varied. These are partly produced by changes of colour during the opening and fading of the flowers, partly by the increase which the petals undergo very noticeably after pollination. In a group of these Cruciferæ of which the Whitlow-Grass, the round-fruited Penny Cress, and the Egyptian Lobularia (*Draba verna*, *Thlaspi rotundatum*, *Lobularia nummulariæfolia* (*cf.* figs. 252 [1, 2, 3]) may serve as types, the originally very tiny white leaves of the corolla increase to twice their size, and adhere to the broad side of the ovary, which has meanwhile become much enlarged, and brown or violet in colour. The ovaries, to which the snow-white petals adhere, grow into young fruits, and then form a wreath, just as in the species of Clover described above, around the younger white flowers, as well as the central green buds. The consequence is that the whole inflorescence is rendered conspicuous, although the leaves of the corolla when it opens are small and insignificant.

In a second group of the Cruciferæ, of which *Thlaspi alliaceum* and *Thlaspi arvense* may be chosen as examples, the ovaries as they mature into fruits are only slightly discoloured, but the green of the sepals changes in the older flowers into yellow. Thus in each corymb white, yellow, and green appear side by side in a varied play of colour. A third group, of which *Alyssum calycinum*, *Draba aizoides* and *Arabis cærulea*, may serve as types, is rendered conspicuous by the bleaching of the sepals and petals after flowering. The petals of *Draba aizoides* and *Alyssum calycinum*, which, while blossoming, were golden yellow, become whitish and adhere to the young green fruits. The petals of *Arabis cærulea* are blue at the commencement of flowering, but fade later on and lie flat on the young fruits, which have meanwhile assumed a violet tint. In these three groups of Crucifers the broad side of the maturing ovary serves as a foil to the pale floral-leaves, which increase in size after fading, and thus a piebald effect is given to the whole inflorescence. In a fourth group, of which the Wild Cress (*Æthionema*) is an example, the young fruits are completely enveloped by the enlarging floral-leaves, and are therefore without significance as regards colour. The contrast is here obtained in the following peculiar manner: The young flowers are supported side by side on short, erect pedicels at the top of a common stem, and their small, expanded petals are all turned with their upper side towards the observer. After fading, the pedicels lengthen, bend sideways, and project horizontally from the common stalk of the whole inflorescence. The petals still grow in length and breadth, and place themselves together like the leaves of a book, so that the side which formerly was the lower one is now turned to the spectator. But, since the upper and under sides of the petals are differently coloured, the young flowers crowded in the centre of the corymb exhibit a different colour from the old ones of

the circumference. This phenomenon is most beautifully shown in species of this genus which grow in the Taurus (*Æthionema grandiflorum* and *diastrophis*) where the white centre of the corymb is surrounded by an ornamental red wreath of older, folded flowers. The species of the genus Bitter Cress (*Cardamine*), which, together with many other Cruciferæ, form a fifth group, agree with the species of Wild Cress just described in regard to the enlargement and folding together of the petals, but in them the contrast is not brought about by the juxtaposition of the colours on the upper and under sides of the petals, but by a change of colour in the sepals. The sepals, originally green, become coloured yellow in the older, horizontally-placed flowers, but the colour of the petals remains unaltered, white or violet. Finally, in the flowers of a sixth group, of which *Kernera saxatilis* (fig. 252 [14]) may serve as an example, the petals of the older flowers do not fold together and do not adhere to the ovary, but retain the position which they had at the beginning of flowering, *i.e.* they always present the upper side to the beholder. But as the flowers get older the ovary swells enormously and becomes coloured a dark purple brown; it pushes itself between the petals, and these (which have increased considerably) now form a white inclosure to the purple fruit. Thus the old flowers at the circumference of the corymb obtain a spotted, conspicuous appearance.

We have now to speak of the colour contrast which comes into play between different kinds of plants growing in the same district, the flowers of which unfold simultaneously. In a meadow studded with thousands of the blue flowers of the *Campanula*, the orange-coloured stars of *Arnica montana* rising up between them show up much more plainly than if these Bell-flowers were not present. The same may be said of the Bell-flowers whose blue colour is materially heightened by the presence of the orange-coloured stars of the Arnica. It might almost be said that the growth of plants side by side with contrasting colours so frequently observed is arranged in the way here indicated, and the change of colour in the flowers of one and the same species in different regions can also be explained by the fact that contrast of colour is so advantageous to the plants in question. Let us suppose that on a meadow where in summer a plant with red flowers—perhaps a Pink—grows in great quantity, a blue Bell-flower has established itself. Some members of it may bear white flowers, as often happens in this plant. Without doubt these white Bell-flowers show up better than the blue from the red Pinks, and therefore have more chance of being visited by insects and of forming fruit and seeds. In course of time the white Bell-flowers will constitute the overwhelming majority, and the meadow will be studded for the most part with white Bell-flower blossoms growing between the Pinks with their red flowers. If the same Bell-flower had established itself in a field in which orange-yellow flowers grew in great numbers, the blue and not the white-flowered plants would have been visited by insects, since they would be the more conspicuous; thus they would multiply and ultimately prevail.

In the neighbourhood of the Brenner *Campanula Trachelium* bears white

flowers, but blue flowers in the valleys of the Eastern Limestone Alps. The long-spurred Violet (*Viola calcarata*) displays a blue corolla on the meadows of the Western Central Alps, and a yellow corolla in the Eastern Alps of Krain. *Astragalus vesicarius* has yellow blossoms in the Tyrolese Vintschgau, violet on the Limestone Mountains of Hungary. *Melittis Melissophyllum*, in the Southern Tyrol, has white flowers only; whilst in Lower Austria and Hungary it has purplish-white flowers. The Alpine Poppy (*Papaver alpinum*) occurs on the débris-slopes of the Lower Austrian and Styrian Limestone Alps with white flowers, in those of the South-Eastern Limestone Alps, in Krain, with deep yellow flowers. *Anacamptis pyramidalis*, on the north side of the Alps, is only seen with deep carmine-red flowers; in the Dalmatian Islands and in Italy it exhibits pale flesh-coloured blossoms. *Anemone alpina*, on the Central Tyrolese Alps, bears chiefly sulphur-yellow flowers; in the Eastern Limestone Alps its flowers are always white. The crested Cow-wheat (*Melampyrum cristatum*) displays pale-yellow bracts on its flower-spikes in the Southern Tyrol, but red ones in Lower Austria and Hungary; indeed a long series of plants might still be mentioned which behave in the same way, *i.e.* in which sometimes this sometimes that colour is the more advantageous to the flower, and becomes the prevailing tint in different regions according to the presence of, and in combination with, other plants.

In the descriptions of floral colour, so far given, green has always been regarded as the one which formed the background or substratum from which the other colours and colour-combinations must stand out if they are to be plainly seen by flying animals. As a matter of fact, the ground-tone of the plant-covering during the period of vegetation is mostly green; but in districts where the trees and bushes strip off their foliage in the autumn, and where throughout the winter and spring a mantle of withered leaves covers the ground, the prevailing tint is brown. Similarly, where in the autumn the grasses and various meadow-weeds also wither and fade, the ground-tone of the plant-covered earth in the following spring is not green but pale-yellow or brown. Against such a background obviously the colour-contrasts become somewhat different. Blue colours show up better from a brownish-yellow than from a green background, and it may depend upon this fact that the flowers of so many plants which emerge in spring from the dry withered leaves are coloured blue. The flowers of *Hepatica triloba*, growing in the depths of light woods, are shown up excellently by their blue colour from the yellow-brown Hazel and Hornbeam leafage, but would scarcely be noticed on a green meadow. On ploughed land the flowers of *Omphalodes verna* can be seen 100 yards off over the pale yellow, faded grasses and foliage of the edge of the wood; while at the same distance against a green background they would stand out much less clearly. The same thing is true of many Boragineæ, which grow in similar places (*Pulmonaria angustifolia, officinalis, Stiriaca, Lithospermum purpureo-cœruleum*), of the Lesser Periwinkle (*Vinca minor*), of the Squill (*Scilla bifolia*), and of many others.

Colour-contrasts which differ from those of the green background of land covered with fresh foliage-leaves are also found in shady woodland spots where

dark-brown humus has accumulated. Above the dark mould of the forest-floor a pale colour, such as that of the Bird's Nest (*Neottia*), of *Monotropa*, and of the Toothwort (*Lathræa*), and other saprophytic and parasitic plants, is plainly visible from a distance. These plants would hardly be noticed in a green meadow.

Zoologists are of opinion that animals, especially those which visit flowers to carry off honey and pollen, possess a highly-developed colour sense, and that the visits which are paid by bees, humble-bees, butterflies, flies, and beetles are materially influenced by the colour of the flowers. Different animals prefer different colours, and there are actually certain insects to which some colours are "pleasing", others "unpleasing". The favourite colour of the honey-bee, for example, is a deep violet-blue; pure blue and violet are also pleasing to it, yellow is less sought after but not avoided. Towards green the bees are indifferent, but red is disliked and shunned and is the "unpleasing" colour as far as bees are concerned. With regard to blue and violet it is quite true that these colours in flowers act as excellent allurements for humble-bees and bees, especially for honey-bees, and this is the more remarkable since, as already mentioned, blue flowers are not by any means the most numerous. We can only accept the views of zoologists as to red up to a certain point, however. Flowers with purple-red or carmine-red colour, as well as all the shades from these to violet, are eagerly visited by bees, and therefore only scarlet-red, cinnabar-red, and the shades leading from them to orange are to be regarded as unpleasing to them.

In a garden bed close in front of the house where I live in summer a patch of *Pelargonium zonale*, called by gardeners Scarlet Geranium, is planted. Near at hand, on the other side of the path, there grows the narrow-leaved Willow-herb (*Epilobium angustifolium*). The scarlet-red flowers of the Geranium and the violet flowers of the Willow-herb open simultaneously. Bees and butterflies swarm and flutter hither and thither over them, but, strangely enough, the butterflies halt on both these plants and do not show especial preference for either. The honey-bees fly past the scarlet flowers with indifference, and turn only to the violet flowers of the Willow-herb. In the Vienna Botanic Gardens the bluish-violet flowers of *Monarda fistulosa* and the scarlet *Monarda didyma* stand side by side with the blue flowers of the Hyssop (*Hyssopus officinalis*). All three blossom together about the middle of July. The honey-bees fly about there in large numbers, but they only visit the Hyssop and violet-flowered *Monarda*, the scarlet flowers of *Monarda didyma* being avoided by them. I purposely here say "avoided" and not "disliked", because it is uncertain whether the absence of bee-visits to scarlet flowers is caused really by an actual dislike of the scarlet colour, or whether it is not rather colour-blindness which is known to be the reason why many human beings do not see red. If we say that the honey-bees do not see the scarlet colour it would be clear why they would pay no visits to the flowers of the Scarlet Geranium and the scarlet *Monarda*. They would not notice them, because the nerve-bundles which correspond to the scarlet colour are wanting in their eyes. This does not contradict the fact that other animals see this colour well, and that

for them a scarlet colour may be an effective means of allurement even from a great distance. Butterflies, as already mentioned, hover over the flowers of the Scarlet Geranium; *Monarda didyma* is industriously visited by a large humble-bee, and various animals are seen to fly to other scarlet-red flowers, especially in tropical regions. Such flowers in particular affect the humming-bird. Indeed it seems that this tiny bird in its search after honey prefers scarlet flowers. Perhaps it depends upon this that plants with scarlet flowers are distributed chiefly in those regions where humming-birds have their home. Certainly it is noteworthy that the scarlet colour is only rarely met with in Asia and Europe, particularly in the Alpine, Baltic, Black Sea, and Mediterranean Floras; whilst an exceptionally large number of such flowers occur in America, particularly in Carolina, Texas, Mexico, the West Indies, Brazil, Peru, and Chili. In the primeval forests of Central America every traveller is struck by the great number of Lianes and Epiphytes of the families Acanthaceæ, Bignoniaceæ, Bromeliaceæ, Cyrtandreæ, and Gesneraceæ, which bear scarlet flowers, and of which we may mention as examples—*Bignonia venusta, Lamprococcus miniatus, Pitcairnia flammea, Nemanthus Guilleminianus, Mitraria coccinea,* and *Beloperone involucrata.* Lobelias, Fuchsias, and Begonias with fiery red cups (*Lobelia cardinalis, fulgens, graminea, splendens, Texensis, Fuchsia coccinea, cylindria, fulgens, radicans, spectabilis, Begonia fuchsioides,* &c.), the scarlet species of Sage which are surrounded by humming-birds (*Salvia coccinea, cardinalis*), the various species of *Alonsoa* and *Russelia* belonging to the Scrophulariaceæ, the remarkable Erythrinas (*Erythrina cristagalli, herbacea, speciosa*), and the Cæsalpinieæ of the genera *Amherstia* and *Brownea* (*Amherstia nobilis, Brownea coccinea* and *grandiceps*), whose flowers are so constructed that their honey can hardly be obtained except by the hovering humming-bird—all these find a home in the American regions above-mentioned. Further observations in tropical regions are required to ascertain whether there are not other flower-visiting animals besides humming-birds and butterflies, especially flies and beetles, which can distinguish scarlet flowers and fly to them; for certain plants, as, for example, the Brazilian Aroids with their large scarlet spathes, *e.g. Anthurium Scherzerianum* (the Flamingo Plant), *A. Andrenum* and *Lawrenceanum,* have no honey, and are consequently disregarded by humming-birds and butterflies.

That scarlet flowers are not visited by the hawk-moths, owlet-moths, and other crepuscular and night-flying animals is obvious, since when twilight falls, scarlet, as well as purple-red, violet, and blue flowers become invisible. At this time only those flowers can be seen which are coloured white or yellow on the side turned towards the flying animals, as, for example, the Evening Primrose (*Œnothera*), the Honeysuckle (*Lonicera Caprifolium*), some Nyctagineæ (*e.g. Mirabilis longiflora*), many Solanaceæ (e.g. *Nicotiana affinis, Datura Stramonium*), numerous Caryophyllaceæ of the genus *Silene* (e.g. *Silene nutans, longiflora, Saxifraga*), various species of *Yucca* and *Calonyction,* and, most of all, the large-flowered Mexican Cactuses of the genus *Echinocactus* and *Cereus,* of which the species known as

"Queen of the Night" (*Cereus nycticalus*) is perhaps the most renowned of all. When dark-coloured flowers are visited at night by insects, for example, those of *Hesperis tristis*, *Pelargonium triste* and *atrum*, it is not in consequence of the colour but of the scent of the flowers, as will be described later on. Without doubt, white is the colour which is not only best seen in the dark, but can be plainly distinguished in bright daylight, and it is, as far as we know, not avoided by a single flower-visiting animal. Even those animals which have a badly-developed sense of colour, and can perhaps only distinguish between light and dark, are able to appreciate white, as it is the lightest of all colours. Yellow flowers are eagerly visited by animals which collect and eat pollen, perhaps because the pollen is usually coloured yellow. Greenish-yellow and brownish-yellow flowers, as, for example, those of the Parsley and the Parsnip, of the Aralia and the Ivy, of the Maple and the Buckthorn, of the Rue and the Sumach (*Petroselinum*, *Pastinaca*, *Aralia*, *Hedera*, *Acer*, *Rhamnus*, *Ruta*, *Rhus*), are especially preferred by flies which swarm over dungheaps and other refuse (e.g. *Lucilia cornicina*, *Onesia sepulcralis*, *Sarcophaga carnaria*, *Scatophaga stercoraria*). This phenomenon has been explained by the similarity of the colours named with those of the dungheap and offal generally. Dark brown must exercise a specially attractive power over wasps. They fly with great haste to brown flowers, especially those whose tint resembles that of decaying pears and other fruit, whilst they will pass by colours which are far more noticeable to other eyes. Flowers of a pale, fawn-red, and dirty violet colour in conjunction with brown, so arranged as to resemble decaying flesh and dead bodies, and such flowers as possess by way of additional attraction a smell of putrefaction, are always visited by carrion-flies and dung-beetles in abundance. It might be thought that the smell alone would suffice to attract these insects; but it must be otherwise, or it is difficult to see why the various Aristolochias, Stapelias, Rafflesias, and Balanophoreæ, which smell like carrion, should bear its colours as well as its scent. It is not easy to decide how much depends upon the colouring, and how much on the scent, and it would be premature to give a definite judgment now. It should be noted generally that the opinions just stated should not be accepted as being entirely free from doubt. Researches on these points are very difficult, and there are so many sources of error that the results may have to undergo many corrections sooner or later. But, on the other hand, all that has been said must not be regarded as quite worthless. This one thing is quite certain—that some animals will show a preference for one colour in a flower, while others will prefer another, and that the absence or presence, the significance or prominence of single floral colours is to be placed on a parallel with the same phenomena in the Animal Kingdom.

It is extremely probable also that in many floral regions the predominance of certain floral colours at various seasons of the year is connected with the distribution of animals in time, since the insects which fly about in spring and summer, and in summer and autumn differ from one another. It has been shown graphically by curves for the region of the Baltic flora that in April and May a white colour predominates, and that from the highest point in May the curve of white gradually

sinks to its lowest point in late autumn. Yellow reaches a first maximum in May, falls somewhat during the summer, and reaches a second maximum in October. The curve of red takes a low position in early spring, rises uniformly through the summer, and reaches its highest point in September. The curves of violet and blue show no large variations through the whole period of vegetation, but two maximal points are to be seen in them, just as in the yellow, one in spring, and the other in autumn.

This particular seasonal change of the prevailing flower-colour, of course, only holds good for the Baltic flora. Even in the adjoining Mediterranean flora the colour-curves are somewhat different, and the deviations are greater still in the flora of corresponding latitudes in North America. Nothing can be said of the predominance of certain colours during the vegetation period in the Alpine flora, for on the heights above the tree-line there is actually no spring and no autumn, only a short summer following a long winter. All the flowers have therefore to blossom in this short time, and all the flower-visiting animals must do their flying about during the short period which is free from snow, if they do not wish to starve. Hardly is the snow melted when there appear almost simultaneously the violet bells of the Soldanellas and the golden flowers of the Cinquefoil (*Soldanella* and *Potentilla*), the white Crowfoot and Androsace, the red Silenes and Primulas (*Ranunculus alpestris, Androsace obtusifolia, Silene acaulis, Primula minima*), the blue Gentians and the yellow Auriculas (*Gentiana acaulis, verna, Primula Auricula*), the heaven-blue Forget-me-not and the yellow Violet (*Myosotis alpestris, Viola biflora*) as well as the Saxifrages in every conceivable colour. On looking at the varied flowers which skirt some streamlet fed by the melting snow, high up on a mountain plateau or it may be in a gully, it will be seen at once that every colour is to be met with woven into a gay and continuous carpet here. White and red, yellow and blue, brown and green stand in varied combination side by side on a hand's-breadth of space. The bees, humble-bees, flies, and butterflies which are dependent on the honey and pollen of these flowers may also be seen in Alpine regions flying about at this same time. If one of these animals should be late, its existence is endangered on account of the briefness of the period of vegetation, for should it not happen that some belated flower blossoms in a hollow where the high-piled winter snow has lingered for a long time, the animal is in imminent risk of perishing from lack of food.

THE SCENT OF FLOWERS CONSIDERED AS A MEANS OF ATTRACTING ANIMALS.

The scents of flowers, like their colours, are very intimately connected with the Animal Kingdom. The scent of foliage, stems, and roots, as mentioned elsewhere (vol. i. p. 431), serves very efficiently to frighten and ward off herbivorous animals; but the scent emitted from the flowers, on the other hand, serves to allure such animals as transfer the pollen from flower to flower and from plant to plant

by their visits, thus rendering them an important service. In the Auricula (*Primula Auricula*), Woodruff (*Asperula odorata*), Rue (*Ruta graveolens*), and Lavender (*Lavandula vera*), the flowers and foliage have the same scent, and here the insects seeking for honey and pollen are allured to the flowers, whilst the flowers and foliage are protected from being devoured by grazing animals by one and the same substance. A uniform distribution of odorous substance over different parts of the same plant is, however, comparatively rare; much oftener the scent of the flowers differs from that of the foliage. Thus the Garlics (*Allium Chamæmoly, Sibiricum, suaveolens*) develop the scent of honey in their flowers which brings insects to visit them, while their leaves have a strong odour of onions which keeps grazing animals at bay. In most Umbelliferæ the flowers have a different scent from the foliage-leaves, stem, and roots. The leaves of the Umbelliferous *Euryangium sumbul* (mentioned on p. 745, vol. i.) smell of musk, the root of the Coriander (*Coriandrum sativum*) gives off an offensive odour of bugs, and the Common Hemlock (*Conium maculatum*) has a repulsive odour of mice. And yet the flowers of these three Umbellifers all have a delicate scent of honey, which allures insects to visit them.

The number of scents is very great. At least five hundred can be distinguished. On attempting to classify them and to state their qualities one meets with a serious difficulty, for language is not rich enough to give names to all the different kinds, and nothing remains but to say that Mignonette flowers have a Mignonette scent, Rue flowers have the scent of Rue, and so forth. The need of bringing this multiplicity into something like order, of placing similar scents together and fixing on a central point round which the others could be grouped, as has been done with the ground tints and ground colours, has long been felt, but hitherto sufficient attention could not be given to the need, because the chemical properties of scents which must serve as the basis for any scientific division are only very imperfectly known. However, in what follows the classification of scents which is attempted does not pretend to completeness nor to infallibility, but is to be regarded solely as a first attempt or preliminary outline to which one can turn provisionally in the naming these scents.

Five groups of floral scents may be conveniently distinguished, *i.e.* the indoloid, aminoid, paraffinoid, benzoloid, and terpenoid scents.

To the first group, the *indoloid* scents, belong those volatile substances which arise from the decomposition of albuminous compounds and diffuse into the atmosphere, and in which one or several benzole nuclei are retained, as well as nitrogen; examples are Leucin and Tyrosin, Skatol and Indol. The group derives its name from the last-named substance. These are developed in the inflorescences of numerous Aroids, in the flowers of all the South African Stapelias, in those of the Balanophoreæ, Rafflesiaceæ, and Hydnoreæ, in the perianths of about 200 Aristolochias, and also in those of some tropical Orchids, as, *e.g.* of *Bolbophyllum Beccarii* of the Malayan flora. Sometimes the scent resembles that of decomposing mammalian flesh, sometimes of rotten fish (*cf.* vol. i. p. 196), sometimes again of decom-

posing animal excreta. The West Indian *Aristolochia Gigas* has the scent of old decaying tobacco, and the red-brown flowers of *Calycanthus* smell like fermenting wine, quite unlike the woody branches, which have a pleasant odour reminding one of cloves. It has already been stated that flowers provided with indoloid scents resemble animal corpses in their colouring, having usually livid spots, violet streaks, and red-brown veins on a greenish or fawn-coloured background.

The *aminoid* scents come next to the indoloid. Under this name are comprised all those volatile substances which diffuse into the air and have an amine as their foundation, either a primary, secondary, or tertiary amine, according as to whether one, two, or all three of the hydrogen atoms of the ammonia are replaced by an alcohol radical. It has been shown that the curious odour of the Hawthorn (*Cratægus*) is due to trimethylamine. It is very probable that in numerous other flowers with similar scent trimethylamine or a related compound—ammonia—is developed. The smell of Hawthorn flowers is repeated with slight modifications in the flower of the Pear (*Pyrus*), the Medlar (*Mespilus*), the Mountain Ash (*Sorbus*), the shrubby Spiræas (*Spiræa ulmifolia, chamædryfolia*, &c.), the Dogwood (*Cornus sanguinea*), the Wayfaring Tree and Guelder-rose (*Viburnum Lantana, Opulus*), the Chestnut (*Castanea*), the Elder (*Sambucus racemosa*), the Traveller's Joy (*Clematis Vitalba*), and the Barberry (*Berberis*). The scent which is liberated from the flowers of the Tree of Heaven (*Ailanthus*), of the Horse-chestnut (*Æsculus Hippocastanum*), of the Flowering Ash (*Fraxinus Ornus*), and of the Evening Primrose (*Œnothera*), resembles that of *Cratægus* more remotely. The flowers of the Ivy (*Hedera*) develop a scent which reminds one of herring-pickle, those of the Alpine Poppy (*Papaver alpinum*), partly of Hawthorn, partly of Musk. Two North American plants, viz. *Pachysandra* and *Sanguinaria*, produce a scent distantly resembling ammonia which proceeds, apparently, from an amine compound. Under this division, finally, should be placed that odour so repulsive to the human olfactory organ which is produced by the flowers of the already-mentioned *Melianthus* (see p. 171).

The third group, that of the *benzoloid* scents, is composed of such as are formed from the so-called aromatic bodies. They are compounds with a benzole nucleus in which the various hydrogens of the benzole are replaced by alcohol and acid radicals. The Eugenol (or oil of cloves) in the flowers of many Pinks (*Dianthus Caryophyllus, plumarius, superbus*), the Cinnamyl-alcohol which smells like Hyacinths, the Salicylic aldehyde in the flowers of the Meadow-sweet (*Spiræa Ulmaria*), the Coumarin in the flowers of the Woodruff (*Asperula odorata*), the Vanilla-like scent in the flowers of the Heliotrope (*Heliotropium*) are all well-known chemical compounds. I would also include with these the scents of the Lilac (*Syringa vulgaris*), Lily of the Valley (*Convallaria majalis*), Mignonette (*Reseda odorata*), Jessamine (*Jasminum officinale*), Auricula (*Primula Auricula*), Honeysuckle (*Lonicera Caprifolium*), Acacia (*Robinia Pseudacacia*), Violet (*Viola odorata*), Cyclamen (*Cyclamen Europæum*), Paulownia (*Paulownia imperialis*), and of Ilang-Ilang (*Cananga odorata*).

It is very remarkable that many of these benzoloid scents are repeated in species of very different plant-families. Clove-scent is apparent not only in the above-named Pinks but also in the flowers of many species of Broom-rape (*Orobanche caryophyllacea, gracilis, lucorum*), in some Orchids (e.g. *Habenaria bifolia, Gymnadenia conopsea*), in the yellow flowers of *Ribes aureum*, in the Narcissus (*Narcissus poeticus*), and in a somewhat modified form in the flowers of *Azalea pontica*. Many Catchflies (*Silene nutans, longiflora*, &c.), the Dame's Violet (*Hesperis tristis*), and the dark-flowered Pelargoniums (*Pelargonium atrum, glauciifolium, triste*, &c.) develop the scent of Hyacinth flowers. It has long been known that the scent of Woodruff is found in the flowers of many Grasses (*Anthoxanthum, Hierochloe*), and mixed with honey-scent in the flowers of the Melilot (*Melilotus*). The scent of Vanilla is very widely distributed. Besides the Heliotrope (*Heliotropium Europæum* and *Peruvianum*) some species of Woodruff (e.g. *Asperula glomerata, cynanchica, longiflora*), the Linnæa (*Linnæa borealis*), the Dwarf Elder (*Sambucus Ebulus*), the small Bindweed (*Convolvulus arvensis*), some Orchids of our upland and alpine meadows (e.g. *Gymnadenia odoratissima, Nigritella nigra*), the alpine Saussurea (*Saussurea alpina*), the alpine Spurge Laurel (*Daphne alpina*), and the Nardosmia (*Nardosmia fragrans*) are provided with vanilla-scent to a greater or less degree. Different, but still resembling Vanilla, is the scent of tropical Orchids of the genus *Stanhopea*, and the exactly similar scent of *Epipogium aphyllum*, which grows in European Pine-forests. Lilac scent is less common, but it is found clearly enough in many allies of the Spurge Laurel (e.g. *Daphne striata* and *pontica*). This is the more strange, since the flowers of these Daphnes, though not even related to the Lilac, resemble Lilac flowers to a surprising extent at first sight. On the other hand, many species of the genus *Syringa*, e.g. *Syringa Emodi*, which grows on the Himalayas, have a scent which differs from that of *Syringa vulgaris* (the Lilac). The Lily of the Valley scent is on the whole rarely met with—only in some Mexican Cactuses, especially in *Echinocactus Tetàni*. Acacia scent is found in a good many Papilionaceæ, as, for example, in *Cladrastis lutea, Cytisus alpinus*, and *Spartium junceum*, and also in the flowers of an Iris (*Iris odoratissima*). Auricula scent, besides in many Primulas allied to *Primula Auricula*, is present in the flowers of the Globe-flower (*Trollius Europæus*). Honeysuckle scent is emitted in the evening from the flowers of all the species allied to *Lonicera Caprifolium*, and also in the flowers of *Ismene*, and of a species of Tobacco (*Nicotiana affinis*). Violet scent is fairly widely distributed. In addition to numerous species of Violet (e.g. *Viola odorata, mirabilis, polychroma*) it is also developed in many Cruciferæ, thus, in the Stocks (*Matthiola annua, incana, varia*, &c.), in the Wallflower (*Cheiranthus Cheiri*), and in the common Dame's Violet (*Hesperis matronalis*). The Snowflake (*Leucojum vernum*), the autumn-flowering fringed Gentian (*Gentiana ciliata*), the Spurge Laurel (*Daphne Laureola* and *Philippi*), the blue Water-lily of the Nile (*Nymphæa cærulea*), and the insectivorous Sarracenia (*Sarracenia purpurea*) emit an unmistakable scent of Violets from their flowers. Cyclamen scent is again

found in the flowers of a Winter-green (*Pyrola uniflora*); *Paulownia* scent in the flowers of *Glycine Chinensis*; and Unona scent in the flowers of *Zaluzianskia lychnidea*.

The acids and alcohols of those hydrocarbons which are known as paraffins differ chemically from the benzoloid scents. The name *paraffinoid* may be given to them. With regard to their composition the best known of these compounds are Valerianic acid yielded by the Valerian scent in the flowers of numerous Valerians, especially of *Valeriana officinalis, montana,* and *saxatilis*; Pelargonic acid, which is closely connected with Rose scents, and especially with that of *Rosa centifolia*; the Oil of Rue which is liberated from the flowers of various Rutaceæ, especially of the Common Rue (*Ruta graveolens*); and the volatile Œnanthic acid which is met with as the wine-flower scent in the flowers of the Vine (*Vitis vinifera*), and of Gleditschias (*Gleditschia triacanthos, Sinensis,* &c.). To this group belong also the Lime scent which diffuses with various modifications from the flowers of different Limes (*Tilia alba, Americana, parvifolia,* &c.), and also from those of *Æsculus macrostachya*; the very widely-distributed Nightshade scent from the flowers of many species of the Thorn-apple (*Datura*), of the Mandrake (*Mandragora*), the *Petunia* and numerous other Solanaceæ, as also from those of the Peony (*Pæonia*), and American *Trillium grandiflorum*. The Elder scent of the flowers of *Sambucus nigra* and *Orchis pallens*, and the hircine odour, resembling caproic acid, which is liberated from the flowers of the Lizard orchis (*Orchis hircina*), and, somewhat modified, from those of *Orchis fragrans* are also to be included.

It is uncertain whether the honey scent of fresh yellow bees'-wax and honey developed in so many flowers belongs to the paraffinoid series or not. Formerly it was thought that myricilalcohol (an alcohol of paraffin) caused this peculiar scent. But it would appear that the purified myricilalcohol is scentless, so that it is therefore possible that the honey scent is due to another compound. At any rate, it is naturally associated with the above-mentioned scents, and can be most conveniently described here. It is a very common, if not the commonest of all flower scents. The fact that it is often combined with others, especially with benzoloids, leads to the formation of many varieties. The scent, which is most like that of honey-filled honey-comb fresh from the hive, is produced by the flowers of the Sloe, Apricot, Cherry, and Almond trees (*Prunus spinosa, Armeniaca, avium, Amygdalus communis,* &c.), of *Herminium*, belonging to the Orchids, of the Buckthorn (*Rhamnus pumila,* &c.), and of the Bugwort (*Cimicifuga fœtida*). A slightly different scent is liberated by the flowers of the Bird Cherry (*Prunus Padus*), the Bedstraws (*Galium Cruciata, vernum, verum*), of the alpine Forget-me-not (*Myosotis alpestris*), and Phlox (*Phlox paniculata*), of *Asclepias* and *Cynanchum*, the Corydalis (*Corydalis cava*), many species of Spurge (*Euphorbia Cyparissias,* &c.), the Willows (*Salix Caprea, daphnoides,* &c.), some Compositæ (e.g. *Cirsium arvense* and *brachycephalum*), numerous Umbelliferæ (e.g. *Angelica officinalis, Heracleum Sphondylium, Meum Mutellina, Pimpinella magna*), many Cruciferæ (e.g. *Alyssum montanum, Erysimum odoratum*), many Tulips and

Garlics (*Tulipa sylvestris, Allium Sibiricum, Chamæmoly*, &c.), of the Buckwheat (*Polygonum Fagopyrum*), and of many others. The sweet scent of the Clover which occurs in species other than the common meadow Clover (*Trifolium pratense*) and in other Papilionaceæ (e.g. *Trifolium resupinatum, Lathyrus odoratus*) is only a form of honey-scent.

The last group consists of scents produced from ethereal oils destitute of oxygen called terpenes; the scents corresponding to them may therefore be called *terpenoids*. The materials which give rise to these scents are found sometimes in special receptacles imbedded in the plant-tissues, sometimes in the enlarged end-cells of the so-called glandular or capitate hairs—for the most part in the region of the stem and foliage, more rarely in the flowers. The best-known terpenoid scent occurring in flowers is that of the Orange-flower, produced by Oil of Neroli, which is obtained by distillation of the flowers of *Citrus Aurantium*; in those of Gardenias (*Gardenia*), of *Pittosporum Tobira*, of the Siberian *Pyrus baccata*, and somewhat modified in the flowers of some Magnolias (e.g. *Magnolia obovata* and *Yulan*); also the Citron scent from Oil of Citron which occurs in the flowers of some species of Thyme (*Thymus citriodorus, montanus*, &c.), more especially in those of Fraxinella (*Dictamnus Fraxinella*), and the scent of Lavender which is produced from the Oil of Lavender present not only in the foliage but also in the flowers of *Lavandula*.

It has already been incidentally mentioned that two kinds of scent are often liberated simultaneously from the same flower, and that the scent of honey, in particular, frequently combines with some other. The identification of the scent is rendered much more difficult under these circumstances, especially as sometimes one, sometimes the other scent predominates according to the time of day. Not unfrequently one hears wholly different opinions about the scent of a flower. One observer thinks it to be vanilla, perhaps, another a violet scent. Both may be right, since two kinds of scent may be actually liberated from the same flower, whilst individuals are frequently unequally susceptible to all odours.

The difficulties of identifying the flower scent are also increased by the fact that a certain amount of imagination is almost unavoidable. Taste and sight may also be at fault. On looking at a Carnation one is immediately reminded of the smell of cloves before the scent has actually reached the nose. It is therefore advisable that the flowers should not be seen while their scent is being identified, and that to examine them one should get a friend to hold them before one's nose after one's eyes are shut.

It is noticeable that similar and closely-allied species of plants often have different scents. Many examples have already been given, amongst others that *Gymnadenia conopsea* has the smell of cloves, and the very similar *Gymnadenia odoratissima* a vanilla scent. Of species of the genus *Daphne, Daphne alpina* has a vanilla scent, *Daphne striata* a lilac scent, *Daphne Philippi* a scent of violets, and *Daphne Blagayana* a clove scent. The closely-allied *Orchis fragrans* and *coriophora* can be at once distinguished by the smell of their flowers. The scents

occurring in different species of *Syringa*, *Tilia*, and *Sambucus* can also be easily recognized. In Roses this phenomenon is even more remarkable. From their scents *Rosa alpina*, *pimpinellifolia*, *arvensis*, *Indica*, *moschata*, *canina*, *Gallica*, *cinnamomea*, *Centifolia*, and *Thea* can be at once distinguished with closed eyes by anyone who has examined the numerous species of this genus even to a limited extent. It is also remarkable that in closely-allied species the flowers of one will smell while those of another will be scentless. *Habenaria montana* has no scent, whilst *Habenaria bifolia* exhales a strong scent of cloves. *Viola tricolor* is scentless, *Viola polychroma* develops a strong violet scent. The flowers of *Primula Lehmanni* have no scent, while those of *Primula Auricula*, which can hardly be distinguished from the former, have a strong Auricula smell. These facts are not without bearing in the theory of specific constitution of protoplasm, as will be discussed later on in the chapter on the Origin of Species, and therefore should be noted here in passing.

We are liable to many erroneous inferences with regard to the perception of flower scent by animals, since our judgment depends mainly on our own sense of smell, and it is very possible, even probable, that the power of smell in flower-visiting animals differs materially from ours. The olfactory sense of man is lodged in a sharply-defined portion of mucous membrane in the upper part of the nasal cavity. There the superficial cells of the mucous membrane join with the end branches of the olfactory nerve in a peculiar net-work, and the scents must act directly on this region if they are to produce the sensation of smell. But this is again only possible if the odorous substances give off fine particles into the air, and if this impregnated air is wafted over the special part of the nasal mucous membrane. It was formerly held that the substances passing thus over the olfactory mucous membrane were dissolved in a fluid and were then distributed in solution. Only in this way could they influence the nerve-endings. But this view is contradicted by a series of facts of which the most important are the following: it is well known that we can smell certain metals whose finely-divided particles break away and enter the nose, although these metals are certainly not soluble in the mucous membrane. We are also able to smell very different scents quickly, one after the other, which would not be the case if the sense of smell were dependent on a previous solution of the odorous substance in the fluid which saturates the mucous membrane. Again it is a remarkable fact that the mucous membrane is altogether absent from the olfactory organ of many animals. The knobs and pegs on the surface of the feelers which form the olfactory organs of insects are indeed connected on one side with gangliose nerve-endings, but they have nothing resembling a mucous membrane which could contain or secrete a fluid, and yet insects are characterized by their fine sense of smell.

The stimulation of the nerve-endings in the olfactory organ cannot therefore be the result of a previous solution of the odoriferous substance, but must be considered as the transference of a movement. It seems as if the molecules of the odorous substance which are present in the air undergo a rotatory, vibrating, or

some kind of swinging movement, and that this movement is transferred to the nerve-endings as soon as the molecules come into contact with the olfactory organ. Since the nerve-endings are not exposed the transference must take place through the portion overlying the nerve-ends, and it must depend upon the structure of this superficial layer which is exposed to the air whether the transference takes place quickly or slowly, completely or only partially. It is necessary that the stimulation of the nerve-endings, which we imagine to be a form of movement, should be conducted to the central organ if it is to be perceived as smell. But now arises this difficult question: Do the various sensations of smell depend upon the fact that different nerve-endings are stimulated by different odorous substances, and that a particular scent, *e.g.* that of Oil of Lavender, is only perceived when those particular nerve-ends are stimulated which are sensitive to the kind of vibration undergone by the molecules of the Oil of Lavender? Or, are they caused directly by the movement of the molecules of any odorous substance being transmitted by any olfactory nerve-fibre to the central organ, and there producing a definite sense of smell? In this case the same nerve-fibre which had just transmitted the vibrations of the lavender oil would be capable in the next moment of transferring to the central organ those belonging to the molecules of chloroform.

The one hypothesis assumes that certain parts of the central organ, as well as the nerve-fibres leading to them, differ essentially from one another in their capability of being stimulated, although they seem to our senses to be of exactly the same structure. One part can only be stimulated by Oil of Lavender and is not affected by chloroform molecules, another part is only set into a corresponding movement by the swinging of chloroform molecules, but is not in sympathy with the particular movement of those of lavender oil. But to favour this hypothesis is to assume an enormously large number of different nerve-endings in the olfactory organ considering the innumerable quantity of different odoriferous substances that exist—even if it be granted that there is a place only for groups of similar substances in the olfactory organ and not for each singly, the individual scents of each group being only produced by the different degree of the stimulation. The other hypothesis assumes that each olfactory nerve-fibre according to its structure is enabled to transmit the different forms of movement which occur at its peripheral end to the central organ. The particular movements of the molecules of lavender oil would not only affect the nerve-ends, but would continue as a specific form of movement through the whole nerve-fibre to the central organ, and would be there perceived as the scent of lavender oil. This same nerve-fibre which had just transmitted the scent of lavender might in the next moment transmit the vibrations of chloroform and produce the chloroform smell. Such conduction resembles that of a telephone at least in this that different words spoken at one end through the same telephone can be heard unaltered at the other end. The assumption of a conduction of specific forms of movement set up by odorous substances from the periphery through the whole nerve-fibre up to the central organ, also renders it necessary to assume that the olfactory nerve-fibres are not stimulated at all by

certain materials. Thus vibrations which exceed the limits of irritability of the olfactory nerves in rapidity produce no smell.

Whichever hypothesis one accepts one comes to the conclusion that a great difference may exist between the sense of smell of men and animals according to the different degree of sensitiveness of their olfactory fibres. Although the molecules of a substance floating in the air stimulate (*i.e.* set in motion) no single nerve-ending in the human olfactory mucous membrane, this does not prove the absence of nerves in the olfactory organ of some animal sensitive to the particular form of motion of these molecules. It might easily happen that one insect would smell Hyacinths but not Roses, while another would smell Roses and not Hyacinths. This conclusion is, however, of importance in explaining the allurement of certain animals to flowers which appear scentless to man, as well as in explaining the phenomenon that many flowers are eagerly visited by one group of insects and are avoided or rather ignored by another. The Virginian Creeper, *Ampelopsis quinquefolia*, so often planted to cover porches, palings, and walls, develops flowers in midsummer which are visited by bees very industriously and eagerly. The colour does not act as an allurement in this case, for the flowers have green corollas, are hidden away under the foliage, and cannot be seen even by good eyes at a little distance. Yet the bees fly thither from all sides in such a way as to leave no doubt that the flowers of the *Ampelopsis* can be perceived by them a considerable way off. Since it is not their appearance it must be their smell which announces their presence! But to men they appear to be quite scentless! The flowers of the Common Bryony (*Bryonia dioica*) are not less remarkable. They occur on two kinds of plants, *i.e.* on one plant are developed only staminate and on the other only pistillate flowers, and since the pollen is not powdery, and therefore not scattered by wind, it must be carried by insects from plant to plant if the ovules are to mature. But the flowers, especially the pistillate ones, are very insignificant, green in colour, with faint smell, and they are half hidden under the foliage. Many insects fly past them without noticing them. They are almost exclusively visited by one of the Hymenoptera, viz. *Andrena florea*, and it can find them even in the most out-of-the-way places. This can hardly be accounted for except by supposing that the scent of Bryony flowers is perceived by these particular bees and not by other insects. To these two examples of insignificant flowers, which appear to men and to many animals to be scentless but which are nevertheless eagerly tracked by certain insects, may be added the common Birthwort (*Aristolochia Clematitis*), the Whortleberry (*Vaccinium Myrtillus*), *Chamæorchis alpina*, the Twayblade (*Listera ovata*), and many others. It is probable that there are also flowers which differ from these in having bright colours contrasting with the green foliage, and in addition exhale a special scent to allure certain animals. It is, of course, hardly possible to speak with certainty. In all these questions we have to deal with observations concerning the relations between insects and flowers in nature, and since many sources of error exist, the conclusions arrived at must be accepted with discretion. As to the so-called "flower fidelity"

of insects, by which is meant the preference of certain kinds for certain flowers, the matter is only mentioned here very generally so far as the scents are concerned, and only the main results of these observations are given.

It may be stated as one of these that the indoloid scents have an attraction for certain flies of the genera *Scatophaga*, *Sarcophaga*, *Onesia*, *Lucilia*, *Pyrellia*, *Calliphora*, *Sepsis*, and *Musca*, and for beetles of the genera *Aleochara*, *Dermestes*, and *Saprinus*, which appear on carrion and excrement; indoloid scents remain unnoticed, on the other hand, by butterflies, bees, and humble-bees. Aminoid scents attract large and small beetles, especially Cetonias, and after them Hymenoptera; butterflies, however, are hardly ever allured by them. The scent of honey acts powerfully on bees and humble-bees; also on butterflies, burnet-moths (*Zygæna*), and on day-flying hawk-moths (*e.g.* the Humming-bird Hawk-moth, *Macroglossa stellatarum*), as well as on small beetles; but insects which are attracted by indoloid scents are not affected by the scent of honey. Certain Hymenoptera which, oddly enough, themselves have paraffinoid scents (viz. species of *Prosopis*), fly to flowers with the same smell. Flowers with the scent of Honeysuckle are frequented by large crepuscular hawk-moths, but this scent has no attraction for beetles. Butterflies will pass over flowers with a Honeysuckle scent without pausing, leading us to think that either the scent is not perceived by them, or that they find it unpleasant.

Many flower scents, especially the paraffinoids, are less easily perceived at their place of origin than at a little distance, which is explained by supposing that the odorous particles liberated from the flowers are acted on by oxygen or aqueous vapour as they diffuse through the air, and that various molecular changes go on in them. But since our knowledge of the chemical properties of scents is still so imperfect we must beware of suppositions of this kind. The phenomenon is most pronounced in the Lime and in the Vine. As one approaches a Lime-tree in full flower the pleasant scent of its blossom is strongest at a distance of about 30 yards; if one comes into the immediate neighbourhood and smells the flowers on its lower branches, the scent is neither so strong nor so pleasant as it was further off. In a journey up the Danube, through the part of the valley called the Wachan, with its Vine-clad slopes, I found the air of the whole valley, even that above the water, so filled with the scent of Vine flowers that it seemed almost impossible they should be so far off. And yet the nearest Vines on the banks were 100 yards above the water, and at least 300 yards from the boat. Afterwards I found when wandering through the vineyards that the smell of the flowers close at hand was much weaker than at a distance, and was forced to the paradoxical opinion that with increasing distance and diffusion over a wider area the scent does not diminish but waxes stronger.

The fact that man can perceive certain odoriferous substances in the finest state of division and at incredible distances paves the way for explaining the so-called animal perception of scents. We speak of this animal perception when we gather from other signs that an animal is able to smell what we cannot at the same

distance. Since it has been already explained that animals can perceive scents which will not stimulate our olfactory nerves at all, it is not wonderful that bees will fly from a distance to the flowers of *Ampelopsis*, although they are not able to see these flowers so far away. They smell the flowers of *Ampelopsis* which are scentless to us at 300 yards, just as we do the flowers of the Vine at the same distance.

Of the multitude of remarkable observations concerning the power of smell in animals only those interest us here which are connected with the visits of insects to flowers; of these, two deserve special mention. Some years ago the Aroid *Dracunculus Creticus* from Cyprus was planted on the edge of a small group of coniferous plants in the Vienna Botanic Gardens. There was no dungheap or decomposing animal matter anywhere in the vicinity, nor was there any trace of carrion-flies or beetles. But when during the summer the large cornet-shaped flower-sheath of this Aroid opened, innumerable carrion-flies and dung-beetles flew thither at once from all sides. The indoloid scent emanating from the flower-sheath was only noticeable by human beings a few yards off, but the animals named must have smelt it many hundred yards away. In a certain part of this same garden there is a plant of Honeysuckle (*Lonicera Caprifolium*), and in summer when twilight falls this is regularly visited by the Convolvulus Hawk-moth (*Sphinx Convolvuli*). These hawk-moths are accustomed, after they have sucked the honey and when the twilight fades into night, to settle near the plant on the bark of old tree-trunks or on fallen leaves, and there they remain with folded wings as if they were benumbed until the next evening. A few summers ago I very carefully picked up one of the pieces of wood which had been chosen as a resting-place by one of these hawk-moths. I marked the moth slightly with cinnabar and brought it, together with the piece of wood on which it remained immovable, to another part of the gardens 300 yards away from the Honeysuckle. When twilight fell the hawk-moth began to wave the feelers which serve it as olfactory organs hither and thither a few times, then stretched its wings and flew like an arrow through the garden towards the Honeysuckle. Shortly after I met the hawk-moth with the cinnabar mark hovering over these flowers and sucking the honey. It had flown straight to the plant, and must have been able to smell the scent of the flowers even at so great a distance.

One of the most remarkable correlations between flower scent and animals is the development of the scent simultaneously with the time of flying of certain insects. The flowers of certain species of Honeysuckle, which are much visited by crepuscular Lepidoptera (*Lonicera Caprifolium, Periclymenum, Etrusca, grata*, &c.), of Petunias (*Petunia violacea, viscosa*, &c.), of *Habenaria bifolia*, and of many other plants, smell very faintly or not at all through the day. After sunset, from about 6 or 7 in the evening until midnight, they give off an abundant odour. Still stranger is the behaviour of the flowers of *Hesperis tristis*, of the dark-flowered Pelargoniums (*Pelargonium triste, atrum*, &c.), and of numerous Caryophyllaceous plants (*Silene longiflora, nutans, viridiflora*, &c.), which are visited by

small nocturnal moths, and give off no scent during the day, but exhale a strong Hyacinth odour at twilight. Similarly the flowers of the common Dame's Violet (*Hesperis matronalis*) smell like Violets in the evening, and those of a species of Woodruff (*Asperula capitata*) smell of vanilla as darkness approaches. On the other hand, many flowers visited during the day by butterflies, bees, and humble-bees become scentless at sunset. The yellow flowers of *Spartium scoparium* only exhale their exquisite acacia scent when the sun is high and the insects named are swarming through the warm air. In the evening there is no trace of the scent. The ornamental Clover, *Trifolium resupinatum*, whose flowers are surrounded by bees, smell strongly of honey in the sunshine, but become scentless as soon as the bees return to their hive at twilight. The same is true of the Grass of Parnassus (*Parnassia palustris*), which only smells of honey in bright sunshine and becomes scentless in the evening. A species of Daphne growing in the Pyrenees (*Daphne Philippi*) liberates a delicate scent of Violets during the day, only ceasing to smell when night falls.

It is sometimes suggested that colour and scent in flowers to some extent mutually exclude one another, so that in cases where the allurement of honey- and pollen-eating insects is brought about by the bright colour of the corolla, the scent is absent, and *vice versa*. This idea is supported by the facts that many flowers with brilliant colouring, which can easily be seen at a distance on account of their large size, have no scent, *e.g.* the flowers of the Cornflower (*Centaurea Cyanus*), the Pheasant's Eye (*Adonis æstivalis* and *flammea*), many Gentians (*Gentiana acaulis, Bavarica, verna*), various species of Lousewort (*Pedicularis incarnata, rostrata,* &c.), the Camellia (*Camellia Japonica*), the Indian Azalea (*Azalea Indica*), and numerous species of *Amaryllis* and *Hemerocallis*; whilst, on the other hand, many plants with small and insignificant flowers, as, for example, the Mignonette (*Reseda odorata*), the Vine (*Vitis vinifera*), the Ivy (*Hedera Helix*), Gleditschia (*Gleditschia triacanthos*), and Eleagnus (*Eleagnus angustifolia*) give off a strong scent which can be perceived at some distance. It might be also pointed out that the oft-mentioned Pelargoniums (*Pelargonium atrum* and *triste*) and *Hesperis tristis*, which bear dirty yellow and dark flowers, indistinguishable to the best sight in twilight, develop a strong Hyacinth odour, which allures numerous small night-flying Lepidoptera. But however conclusive these examples may be, there are many others of the opposite kind, *i.e.* of bright and noticeable colours, occurring not infrequently in conjunction with strong scents. Roses, Pinks, and Stocks, many tropical Orchids, Magnolias, Narcissi and the large-flowered Rhododendrons of the Himalayas show at least that the view mentioned has not a universal application.

OPENING OF THE PASSAGE TO THE INTERIOR OF THE FLOWER.

The removal and transmission of pollen by animals can obviously only take place when the perianth-leaves, under whose protection the pollen and stigmas are matured, permit of access to the base of the flower. I have altered the usual

expression "Opening of Flowers" in the headline above, since flowers exist to which the term "open" does not apply. The flowers of the Snapdragon and Toadflax (*Antirrhinum* and *Linaria*) never open spontaneously; but the insects which frequent them for honey have to open the door for themselves by pushing down the lower lip. So, also, in the flowers of Papilionaceæ. In the bud the uppermost petal or standard incloses the four others like a mantle; only when the pollen is mature, and has been discharged from the anthers, does the standard fold back, and one says the plant is in flower. But still no opening is to be seen, access to the honey remains now, as before, hidden, and insects must introduce their probosces between the folded petals. Still, from a consideration of these and other cases, it may be urged that there is essentially an opening of what was closed in the bud, a giving of access to the interior of the flower, so that perhaps the headline above meets the case.

The arrangement of the petals in the flower-bud is determinate for individual cases, and is often made use of by descriptive botanists as a useful character for discriminating families and genera. This manner of folding is known as *Æstivation*, of which several forms are distinguished. (1) The *crumpled* æstivation, characteristic of the Poppy, Cistus, and Pomegranate (*Papaver*, *Cistus*, and *Punica*). The petals here, to quote Grew, "are cramb'd up within the *Empalement* [*i.e.* calyx] by hundreds of little *Wrinkles* or *Puckers*; as if Three or Four fine *Cambrick Hankcherchifs* were thrust into ones *Pocket*". (2) *Plaited* or *plicate* æstivation, where a funnel- or bell-shaped corolla is folded in regular, longitudinal pleats, as in Venus's Looking-glass (*Specularia*). (3) When the band-like corollas of many Composites, as the Salsify and Dandelion (*Tragopogon* and *Taraxacum*) are rolled up longitudinally into a tube closed above by five little teeth, one speaks of a *convolute* æstivation; (4) when, as in Umbelliferæ and many Caryophyllaceæ, the petals are rolled up from apex to base, of a *circinate* æstivation. (5) Sometimes the folded or unfolded petals are so placed one upon the other, that on one side each is in contact with the adjacent petal of that side, and on the other side with that of the other, the whole corolla appearing spirally twisted. This condition is known as *contorted* æstivation, of which examples are the Wood-sorrel (*Oxalis*), Periwinkle (*Vinca*), and other Apocynaceæ, Solanaceæ, and Convolvulaceæ. (6) The commonest form of æstivation is that in which the petals or lobes of a united corolla overlap like tiles on a roof, without being twisted, however. The outmost petal covers all the rest, or a pair of outer petals inclose a pair of inner ones. This, the *imbricate* æstivation, is characteristic of the Apple, Rose, Buttercup, and Anemone, also, in a modified form, of Papilionaceæ and Pinks. (7) In a number of plants, e.g. *Asarum*, Lilac, and Vine, the petals do not overlap, but touch merely by their margins, and form a sort of dome or vault. This is known as *valvate* æstivation. Among these kinds of æstivation various combinations occur, thus the Poppy in addition to being crumpled is imbricate, and several Pinks (*Dianthus neglectus*, *glacialis*, &c.) with imbricating petals are also convolute. It further often happens that the leaves of the calyx have an æstivation differing from that of the corolla. Here, again, the Poppy is an instance in point, its calyx is valvate, and its corolla imbricate and crumpled.

In bilabiate corollas, although the individual parts vary a good deal, the imbricate æstivation is constant, though numerous modifications obtain which cannot be described at length here. Two fairly frequent cases, however, must be described, appertaining to the ringent and personate corollas, to be referred to by and by. In the ringent corolla the upwardly-bent median lobe of the lower lip is placed like a lid in front of the corolla-tube, and upon it lie the two lateral lobes of the same lip; these are covered by the downwardly bent upper lip. In the buds of the Germander (*Teucrium*), the middle lobe of the lower lip is bent up to such an extent that it covers over the anthers like a dome, whilst in those of the flowers of the scrophularineous Snapdragon and Toadflax (*Antirrhinum* and *Linaria*) complete closure of the flower is caused by an inflated portion of the lower lip (the so-called palate), this is covered by the upwardly-directed, central lobe of the lower lip, and this again by the two downwardly directed lobes of the upper lip.

All these obstacles, however, to access to the interior of the flower are soon removed. The petals, having served as protective wrappers to the bud, fall away on the opening of the flower in cases where they have no further function to discharge. This condition, truly, is a rare one, but occurs in the Vine (*Vitis*). The petals here are valvate in the bud and form a dome-like covering to the stamens and ovary; they are green in colour, not readily distinguishable from the foliage, and of little value as attractive organs for insects. Under these circumstances it is of advantage that they should be got rid of quickly. This is accomplished as follows. The petals separate from the flower at the base, each rolls up spirally, and they remain hanging together by their apices for a while like a hood, which is ultimately thrown off in consequence of the expansion of the stamens.

This class of opening of flowers is, as stated, rare. In the great majority of cases the petals play a definite part in the later stages of flowering, and are consequently retained. Access to the interior of the flower is brought about by the development between the petals of wide slits as in the Rampion (*Phyteuma*), or, in ordinary cases, by the entire separation of their free ends from one another; the petals, in fact, spread out, and sometimes even become folded back. This separation, of course, corresponds to the position which the petals previously occupied in the bud. Where the æstivation is valvate, the apices of the petals simply fold back like valves; where it is imbricate, the petals become disentangled; where it is plaited or crumpled, the folds or inequalities become smoothed out. Spirally-twisted buds become untwisted, and it may frequently be observed that two or even three different sorts of movement are necessary for a flower to open.

In this way, in many cases, only a somewhat circumscribed opening arises, leading down to the expanded or tubular interior portion of the flower. In others, again, the whole flower opens widely like a cup or saucer, as in Roses, Anemones, and Peonies.

The separation of the petals usually happens very quickly. In the Honeysuckle (*Lonicera Caprifolium*) opening begins with the folding back of the lowest lobe of the corolla, followed by a similar movement of the others, the stamens become liberated and spread like the fingers of a hand. The whole series of movements can

be readily followed, and lasts barely two minutes. Still more rapid is the opening of the Evening Primrose (*Œnothera grandiflora*). The petals spring apart quite suddenly and stretch themselves out within half a minute. If ever the term "bursting open" applies to a flower-bud, it does so here. In several tropical Orchids, also, the parts separate quickly enough for the movements to be readily visible. Thus, in the beautiful *Stanhopea tigrina*, the whole process only occupies three minutes. It is worth mentioning, that during the opening of this flower, a distinct noise is heard, not unlike the report caused by the bursting of the inflated calyx of the Bladder-campion.

There are flowers which open so early in the morning that they greet the first rays of the rising sun with fully expanded corollas. That common garden climber, *Ipomœa purpurea*, opens its buds at 4 a.m. Wild Roses, also, open between 4 and 5 a.m. Between 5 and 6 many species of Flax (*Linum perenne* and *Austriacum*) open. Between 6 and 7, Willow-herbs (*Epilobium angustifolium* and *collinum*), between 7 and 8, *Convolvulus arvensis* and *tricolor*. Between 8 and 9, many Gentians, Speedwells, and Wood-sorrels, and the frequently-cultivated Himalayan Cinquefoil (*Potentilla atrosanguinea*). Between 9 and 10 most Tulips and Opuntias open; between 10 and 11, the Centaury (*Erythræa*) and Chaffweed (*Centunculus*). Between 11 and 12, *Potentilla recta*. From noon till evening comes a long interval. No plant is known in our latitude which, under ordinary circumstances, opens during the afternoon. Towards sunset, however, it recommences. About 6 p.m. the Honeysuckle opens, shortly followed by the Evening Primrose and Campion. Between 7 and 8 p.m. *Hesperis matronalis* and *tristis*, the Marvel of Peru (*Mirabilis Jalapa*), a few Catchflies (*Silene noctiflora* and *vespertina*) and several Thorn-apples (*Datura Stramonium*). Between 8 and 9 more Catchflies (*Silene longiflora*, *Saxifraga*, *Vallesia*), a Woodruff (*Asperula glomerata*), and a species of Tobacco (*Nicotiana affinis*). Between 9 and 10, the Queen of the Night (*Cereus nycticalus*, the Mexican cactus) opens.

As it is with the commencement, so is it with the end of flowering; each happens at a definite time, and every flower endures for a determinate period. Flowers which are only open for a single day are termed *ephemeral* flowers. The annexed table shows the hours of opening and closing of a series of ephemeral flowers.

Name of Plant.	Opens at	Closes at	Name of Plant.	Opens at	Closes at
Allionia violacea	3–4 A.M.	11–12 A.M.	*Portulaca grandiflora*	8–9 A.M.	6–7 P.M.
Roemeria violacea	4–5 „	10–11 „	*Calandrinia compressa*	9–10 „	1–2 „
Cistus Creticus	5–6 „	5–6 P.M.	*Drosera longifolia*	9–10 „	2–3 „
Tradescantia Virginica	5–6 „	4–5 „	*Arenaria rubra*	10–11 „	3–4 „
Iris arenaria	6–7 „	3–4 „	*Portulaca oleracea*	10–11 „	3–4 „
Hemerocallis fulva	6–7 „	8–9 „	*Spergula arvensis*	10–11 „	3–4 „
Convolvulus tricolor	7–8 „	5–6 „	*Sisyrinchium anceps*	11–12 „	4–5 „
Oxalis stricta	8–9 „	3–4 „	*Mirabilis longiflora*	7–8 P.M.	2–3 A.M.
Hibiscus Trionum	8–9 „	11–12 A.M.	*Cereus grandiflorus*	8–9 „	2–3 „
Erodium Cicutarium	8–9 „	4–5 P.M.	*Cereus nycticalus*	9–10 „	2–3 „

The number of hours during which these flowers remain open are as follows:—

	Hours.		Hours.		Hours.
Hibiscus Trionum	3	*Sisyrinchium anceps*	5	*Iris arenaria*	9
Calandrinia compressa	4	*Roemeria violacea*	6	*Convolvulus tricolor*	10
Portulaca oleracea	5	*Oxalis stricta*	7	*Tradescantia Virginica*	10
Drosera longifolia	5	*Mirabilis longiflora*	7	*Portulaca grandiflora*	10
Arenaria rubra	5	*Cereus grandiflorus*	7	*Cistus creticus*	12
Spergula arvensis	5	*Allionia violacea*	8	*Hemerocallis fulva*	14
Cereus nycticalus	5	*Erodium Cicutarium*	8		

From these tables we see that plants with ephemeral flowers may be arranged in two groups; those in which the flowers open between early morning and noon, and those which open at the commencement of twilight or during the night. The latter may be distinguished as "night-flowerers".

Included with the ephemeral flowers are such as open in the evening between seven and eight o'clock, and remain open the whole night and following morning till past midday, or even till evening. For the most part, these close within twenty-four hours of their opening. To these belong several species of Thorn-apple and Evening Primrose, Morina, the Marvel of Peru, and a few Cactuses (*Datura Metel* and *Stramonium*, *Œnothera biennis* and *grandiflora*, *Morina Persica*, *Mirabilis Jalapa*, *Echinocactus Tetani*).

Another series of plants have the peculiarity that their flowers open for the first time during the morning, close at evening, and open again the following morning, but fade or fall during the afternoon of the second day. Examples are many: Papaveraceæ, many species of Flax, the Raspberry, a few Cinquefoils and Cactuses (*Glaucium corniculatum* and *luteum*, *Papaver alpinum*, *Linum tenuifolium*, *Rubus Idæus*, *Potentilla recta*, and *Opuntia nana*).

The duration of flowering (*i.e.* period of persistence of single flowers) in plants which keep open for more than a single day is indicated, for selected examples, in the annexed table:—

2 Days.

Centunculus minimus.
Dianthus prolifer.
Epilobium collinum.
Geranium pratense.
Papaver somniferum.
Potentilla atrosanguinea, &c.
Rosa arvensis, &c.
Saponaria Vaccaria.
Sinapis arvensis.
Veronica aphylla, &c.

3 Days.

Lonicera Caprifolium.
Potentilla formosa.
Agrimonia Eupatorium.
Aphyllanthes monspeliensis.
Galium infestum, &c.
Helianthemum alpestre, &c.

4 Days.

Lychnis diurna.
Sagina saxatilis.
Sedum atratum.
Scilla liliohyacinthus.
Telephium Imperati.
Sanguinaria Canadensis.

5 Days.

Eschscholtzia Californica.
Fritillaria meleagris.
Scilla Sibirica.
Erythræa Centaurium.
Linum viscosum.

6 Days.

Digitalis purpurea.
Erythræa pulchella.
Hemerocallis flava.
Lilium album.
Oxalis lasiandra.

7 Days.

Ranunculus acer, &c.
Pelargonium zonale, &c.

8 Days.

Eranthis hiemalis.
Hepatica triloba.
Parnassia palustris.
Saxifraga bryoides.

10 Days.

Cyclamen Europæum.

12 Days.

Crocus sativus.
Saxifraga Burseriana.

18 Days.	40 Days.	60 Days.
Vaccinium Oxycoccos.	*Cypripedium insigne.*	*Oncidium aruentum.*
	Odontoglossum (many).	70 Days.
30 Days.	50 Days.	*Cypripedium villosum.*
Cattleya labiata.	*Epidendrum Lindleyanum.*	80 Days.
Vanda cærulea.	*Phalænopsis grandiflora.*	*Odontoglossum Rossii.*

The duration of flowers varies then, in different species, from three hours to eighty days. These remarkable differences are connected with the amount of pollen produced in the flowers, and with the number of flowers on each plant. They also depend on whether or no the stigma is entirely dependent on insects for pollen. Flowers with numerous stamens and ample pollen, as for instance, Poppies, Cistuses and Portulacas, have but a brief duration, whilst on the other hand, such as have but a single stamen, *e.g.* most Orchids, remain fresh often for weeks. In plants which produce but a single flower throughout the year, as the Snowdrop, the one-flowered Winter-green (*Pyrola uniflora*), Herb Paris and *Trillium*, or at most two or three, as in the Lady's Slipper Orchid (*Cypripedium Calceolus*), and in tropical Orchids of the genera *Oncidium*, *Stanhopea*, and *Cattleya*, the flowers persist fresh and open for long periods. It may happen also that in consequence of unfavourable climatic conditions flowers may be deprived of insect-visits for many days at a time. In the case of flowers so constituted that in the absence of insects no production of seeds is possible, it follows that in some years the whole object of flowering (where but a single or very few flowers are produced) will be jeopardized. It is obviously of advantage to flowers of this kind that they should be able to hold out for a considerable period. The longer they persist the better is their chance of being visited by insects bringing pollen from other plants.

Let us now take the other extreme, a plant producing numerous flowers, one after the other, in the course of a year, flowers which are able in the absence of insects to pollinate themselves. Here the duration of each flower need be only very short. Notwithstanding the short duration of the flowers the plant remains in blossom for weeks or months. The Spiderworts (*Tradescantia crassula, Virginica*, &c.) have ephemeral flowers, but they go on producing them for eight weeks, during the whole of which time the plants are daily provided with new ones. The same holds good in most Crucifers, Cistuses, Rock-roses (*Helianthemum*), Droseras, &c. The last-mentioned open their flowers only under very favourable conditions of weather, and then only every other day. At any rate, for *Drosera longifolia* it has been shown that, even in the finest weather, a flower-bud opens on alternate days only. Thus we see that pretty much the same result is accomplished in the two classes; in those plants possessing numerous, ephemeral flowers, and in those with solitary, long-persisting ones.

It has already been explained (p. 107) that in localities where a heavy precipitation of dew obtains, flowers which remain open for long periods are liable to a saturation of their pollen during the night, and that many protective arrangements prevail to minimize this danger. One of the most commonly occurring of these

contrivances is the closing of the flowers at night. The petals fold inwards and become furled in the same positions as they occupied in the bud. Indeed, one may say that the flower becomes a bud again. When consistent with the advantages accruing from insect-visits, flowers close in the evening and only open again next day when the danger of wetting by dew is past. In a great number of cases this periodic opening occurs at the same hour as that at which the flower-bud originally opened. Many flowers open but once again, others twice, thrice, or four times on successive days—the Meadow Saffron daily for twelve days. As soon as any particular kind of insect begins to swarm, those flowers, whose structure is adapted to visits from the variety of insect in question, open. Similarly, when the insects retire to rest, the flowers close lest the pollen be exposed to needless danger. In other words, the flowers of many plants *open and close periodically.*

This remarkable phenomenon has for a long time attracted the attention of Botanists, and Linnæus devised his so-called Floral Clock on the basis of his long-continued observations at Upsala. In this he grouped together plants according to the hours at which they opened and closed their flowers, and ascertained, for every hour of the day, what species were doing either the one or the other. Not only were simple, isolated flowers laid under contribution for this purpose, but the complex heads (capitula) of Composites also, since these periodic movements are very conspicuous in them. True, in Composites it is not the petals of a flower which open and shut, but the flowers (florets) of a head; still the cause and effect are here identical with those in ordinary flowers, and Composites were rightly included in the Floral Clock. If the plants which open and close their flowers periodically be cultivated apart, it is possible to determine the time of day by careful observation in this part of the garden. Formerly, the attempt was often made in Botanic Gardens to construct such a Floral Clock, but never with success, because the plants enumerated by Linnæus do not all flower at the same season. Later, when other fields of Botanical activity came into vogue, it was abandoned as a children's game. Consequently the Floral Clock of Linnæus has fallen into oblivion, and the younger generation of Botanists hardly knows its name. For my own part, I am inclined to give this Clock some consideration, as it has a bearing on several important questions in the life of plants. To recall it to memory, it is annexed below in the table which follows. It was constructed for Upsala, 60° north lat.

3–5 A.M.		5–6 A.M.		7 A.M.	
Tragopogon pratense	open.	*Crepis alpina*	open.	*Anthericum ramosum*	open.
		Rhagadiolus edulis	„	*Calendula pluvialis*	„
4–5 A.M.		*Taraxacum officinale*	„	*Lactuca sativa*	„
Cichorium Intybus	„	6 A.M.		*Leontodon hastile*	„
Leontodon tuberosum	„	*Hieracium umbellatum*	„	*Nymphæa alba*	„
Picris hieracioides	„	*Hypochæris maculata*	„	*Sonchus Lapponicus*	„
5 A.M.		6–7 A.M.		7–8 A.M.	
Hemerocallis fulva	„	*Alyssum utriculatum*	„	*Mesembryanthemum barbatum*	„
Papaver nudicaule	„	*Crepis rubra*	„	*Mesembryanthemum linguiforme*	„
Sonchus oleraceus	„	*Hieracium murorum*	„		
		Hieracium Pilosella	„		
		Sonchus arvensis	„		

8 A.M.
Anagallis arvensis.....open.
Dianthus prolifer..... „
Hieracium Auricula..... „

8–10 A.M.
Taraxacum officinale..... shut.

9 A.M.
Calendula arvensis.....open.
Hieracium chondrilloides... „

9–10 A.M.
Arenaria rubra..... „
Mesembryanthemum crystallinum..... „
Tragopogon pratense..... shut.

10 A.M.
Cichorium Intybus..... „
Lactuca sativa..... „
Rhagadiolus edulis..... „
Sonchus arvensis..... „

10–11 A.M.
Mesembryanthemum nodiflorum.....open.

11 A.M.
Crepis alpina..... shut.

11–12 A.M.
Sonchus oleraceus..... shut.

NOON.
Calendula arvensis..... „
Sonchus Lapponicus..... „

1 P.M.
Dianthus prolifer..... „
Hieracium chondrilloides... „

1–2 P.M.
Crepis rubra..... „

2 P.M.
Hieracium Auricula..... „
Hieracium murorum..... „
Mesembryanthemum barbatum„

2–3 P.M.
Arenaria rubra..... „

2–4 P.M.
Mesembryanthemum crystallinum..... „

3 P.M.
Leontodon hastile..... „
Mesembryanthemum linguiforme..... „
Mesembryanthemum nodiflorum..... „

3–4 P.M.
Anthericum ramosum..... shut.
Calendula pluvialis..... „
Hieracium Pilosella..... „

4 P.M.
Alyssum utriculatum..... „

4–5 P.M.
Hypochæris maculata..... „

5 P.M.
Hieracium umbellatum..... „
Nyctago hortensis.....open.
Nymphæa alba..... shut.

6 P.M.
Geranium triste.....open.

7 P.M.
Papaver nudicaule..... shut.

7–8 P.M.
Hemerocallis fulva..... „

9–10 P.M.
Cactus grandiflorus.....open.
Silene noctiflora..... „

MIDNIGHT.
Cactus grandiflorus..... shut.

To the above clock, adapted to the latitude of Upsala, I append a second, based on long-continued observations at Innsbruck (47° north lat.), 13° south of Upsala.

4–5 A.M.
Rosa arvensis (June).....open.

5–6 A.M.
Rosa rubiginosa (June)..... „
Solanum nigrum (July)..... „

6–7 A.M.
Anoda hastata (July)..... „
Cichorium Intybus (July)... „
Crepis pulchra (July)..... „
Dianthus neglectus (July)... „
Gallasia villosa (July)..... „
Hieracium amplexicaule (July)..... „
Hieracium aurantiacum (July)..... „
Lactuca perennis (August).. „
Lampsana communis (July) „
Linum grandiflorum (July) „
Linum viscosum (July)..... „
Mulgedium Plumieri (July) „
Ranunculus acer (July)..... „
Solanum tuberosum (July).. „
Sonchus oleraceus (June)... „
Taraxacum officinale (June) „
Tragopogon floccosus (July) „
Tragopogon orientalis (July) „

7–8 A.M.
Campanula Trachelium (July) op'n
Carlina acaulis (August)... „
Carlina vulgaris (August).. „
Crepis rubra (August)..... „
Gentiana acaulis (May)..... „
Geranium lucidum (July)... „
Gilea tricolor (July)..... „
Hedypnois tubiformis (July) „
Hieracium Pilosella (July).. „
Hypecoum grandiflorum (July)„
Hypochæris maculata (June) „
Lactuca muralis (July)..... „
Oxalis Valdiviana (July)... „
Sonchus arvensis (August).. „
Specularia Speculum (July) „
Tolpis barbata (August).... „

8–9 A.M.
Adonis vernalis (April)..... „
Brassica oleracea (Sept.).... „
Diplotaxis tenuifolia (Sept.) „
Gentiana asclepiadea (Aug.) „
Gentiana cruciata (July)... „
Gentiana utriculosa (June). „
Geranium columbinum (Aug.)„
Helianthemum alpestre (June)„
Isopyrum thalictroides (April) op'n
Lactuca sativa (Aug.)..... „
Lactuca Scariola (Sept.).... „
Mamillaria glochidiata (Aug.)„
Nymphæa alba (Aug.)..... „
Ornithogalum Narbonense (July)..... „
Oxalis lasiandra (Aug.)..... „
Veronica Persica (June).... „

9–10 A.M.
Anagallis arvensis (July)... „
Anemone Hepatica (April).. „
Anemone nemorosa (April).. „
Calendula officinalis (Sept.) „
Colchicum autumnale (Sept.) „
Crepis pulchra (July)..... shut.
Crocus aureus (March).....open.
Draba verna (March)..... „
Eranthis hiemalis (March).. „
Eschscholtzia Californica (June)..... „
Gallasia villosa (July)..... shut.
Oxalis Acetosella (April)....open.
Tulipa sylvestris (May)..... „
Tussilago Farfara (April).. „
Veronica Chamædrys (May) „

10–11 A.M.

Abutilon Avicennæ (July)...open.
Anemone Pulsatilla (March) „
Anemone vernalis (March).. „
Centunculus minimus (Aug.) „
Erythræa pulchella (Aug.).. „
Lampsana communis (July) shut.
Tragopogon floccosus (July) „
Tragopogon orientalis (July) „

11–12 A.M.

Crocus lævigatus (Oct.).....open.
Hieracium amplexicaule (July) ..... shut.
Mesembryanthemum crystallinum (July) .....open.
Nicandra physaloides (July) „
Sternbergia lutea (Oct.)..... „

12–1 P.M.

Sonchus arvensis (Aug.)..... shut.

1–2 P.M.

Hieracium Pilosella (July). „
Lactuca sativa (Aug.)..... „
Sonchus oleraceus (July).... „

2–3 P.M.

Cichorium Intybus (Aug.)... „
Hedypnois tubiformis (July) „
Lactuca muralis (July)..... „
Mamillaria glochidiata (Aug.)„
Solanum tuberosum (July).. „
Taraxacum officinale (June) „

3–4 P.M.

Anagallis phœnicea (July).. „
Erythræa pulchella (Aug.).. „
Eschscholtzia Californica (July) ..... shut.
Gentiana utriculosa (July).. „
Helianthemum alpestre (June) „
Hieracium aurantiacum (July) ..... „
Hypecoum grandiflorum (July) ..... „
Lactuca Scariola (Sept.) ... „
Nicandra physaloides (July) „
Ornithogalum Narbonense (July) ..... „
Oxalis Valdiviana (July)... „
Specularia Speculum (July) „

4–5 P.M.

Calendula officinalis (Sept.) „
Centunculus minimus (Aug.) „
Crocus aureus (March)..... „
Crocus lævigatus (Oct.)..... „
Diplotaxis tenuifolia (Sept.) „
Geranium columbinum (Aug.) „
Isopyrum thalictroides (April) „
Linum grandiflorum (July) „
Linum viscosum (June)..... „
Mesembryanthemum crystallinum (July) ..... „
Oxalis lasiandra (June)..... „

5–6 P.M.

Abutilon Avicennæ (July)... „
Adonis vernalis (April)..... „
Anemone Hepatica (April).. „
Anemone nemorosa (April).. „
Anemone Pulsatilla (March) „
Anemone vernalis (March).. „
Colchicum autumnale (Sept.) „
Draba verna (March)..... „
Gentiana asclepiadea (Aug.) shut.
Lactuca perennis (Aug.)..... „
Oxalis Acetosella (April) ... „
Sternbergia lutea (Oct.)..... „
Tulipa sylvestris (May)..... „
Tussilago Farfara (April).. „
Veronica Chamædrys (May) „
Veronica Persica (June)..... „

6–7 P.M.

Anoda hastata (July)..... „
Campanula Trachelium (July)„
Carlina acaulis (Aug.)..... „
Crepis rubra (July)..... „
Dianthus neglectus (July)... „
Eranthis hiemalis (March).. „
Gentiana acaulis (May)..... „
Hypocheris maculata (June) „
Silene Saxifraga (July)..... open.

7–8 P.M.

Carlina vulgaris (Aug.)..... shut.
Gentiana cruciata (July)... „
Geranium lucidum (July)... „
Gilea tricolor (July)..... „
Nymphæa alba (Aug.)..... „
Ranunculus acer (June)..... „
Silene Vallesia (July).....open.
Tolpis barbata (Aug.)..... shut.

8–9 P.M.

Brassica oleracea (Sept.).... „
Mulgedium Plumieri (July) „
Rosa arvensis (June) ..... „
Rosa rubiginosa (June)..... „
Silene nutans (June).....open.
Solanum nigrum (Sept.).... shut.

In the tables below are collated a few species whose times of opening and closing have been recorded for both Upsala and Innsbruck.

OPENING OF FLOWERS AT UPSALA AND INNSBRUCK.

NAME OF PLANT.	AT UPSALA.	AT INNSBRUCK.	DIFFERENCE IN HOURS.
Cichorium Intybus	4– 5 A.M.	6– 7 A.M.	2
Hemerocallis fulva	5 „	6– 7 „	1–2
Sonchus oleraceus	5 „	6– 7 „	1–2
Taraxacum officinale	5– 6 „	6– 7 „	1
Hypocheris maculata	6 „	7– 8 „	1–2
Sonchus arvensis	6– 7 „	7– 8 „	1
Lactuca sativa	7 „	8– 9 „	1–2
Nymphæa alba	7 „	8– 9 „	1–2
Anagallis arvensis	8 „	9–10 „	1–2
Arenaria rubra	9–10 „	10–11 „	1

CLOSING OF FLOWERS AT UPSALA AND INNSBRUCK.

NAME OF PLANT.	AT UPSALA.	AT INNSBRUCK.	DIFFERENCE IN HOURS.
Taraxacum officinale	8–10 A.M.	2–3 P.M.	5–6
Cichorium Intybus	10 „	2–3 „	4–5
Lactuca sativa	10 „	1–2 „	3–4
Sonchus arvensis	10 „	12–1 „	2–3
Sonchus oleraceus	11–12 „	1–2 „	2
Arenaria rubra	1– 3 P.M.	3–4 „	1
Hypochæris maculata	4– 5 „	6–7 „	2
Hemerocallis fulva	7– 8 „	8–9 „	1
Nymphæa alba	5 „	7–8 „	2–3

From a perusal of these tables it appears that flowers both open and close earlier in the day at Upsala than at the more southerly situated Innsbruck. This result, especially the earlier opening, is probably connected with the fact that the sun during the flowering-season of the plants in question rises about an hour and a half earlier at Upsala than at Innsbruck.

With this difference in time of opening of flowers, the results of observations carried out in mountainous districts on plants which extend from the low warm valleys up into the hills entirely harmonize. The Hepatica (*Anemone Hepatica*) blooms on the valley-floor at Innsbruck (560 metres) in March, at a time when the sun rises at 6 a.m., its flowers opening each day between 9 and 10 a.m. In the mountain glens, south of Innsbruck, at a height of 1560 metres above the sea-level, it blossoms in May, at a time when the sun rises at 5 a.m. Here its flowers open between 8 and 9 a.m. *Lampsana communis* and *Sonchus arvensis* blossom in July in the meadows of the Innthal (560 metres); in the adjacent Gschnitzthal (660 metres higher) in August. The sun rises at Innsbruck in July at 4·30, and the capitula of these two plants open in the Innthal between 6 and 7 a.m.; in August the sun rises about an hour later, and the same plants open correspondingly in the highly-situated Gschnitzthal also an hour later, *i.e.* between 7 and 8 a.m.

Several ornamental garden plants are indefatigable in their blossoming. For months on end flowers upon flowers are produced, only ceasing with the on-coming of winter. As an example *Catananche cærulea* may be instanced; at Vienna it remains in flower from the end of June till the end of October. Its capitula show a periodic opening and closing, but they differ in the hour at which they execute their movements according to the season. At the end of June and beginning of July they open between 4 and 5 a.m., in August and in the first half of September between 5 and 6, whilst in the latter part of September and beginning of October they open between 6 and 7 a.m. Finally, in the widely-distributed Dandelion (*Taraxacum officinale*), to be met with in isolated examples flowering in spring, summer, and autumn, the same thing may be observed. In May it opens between 7 and 8, at midsummer between 6 and 7, in August between 7 and 8, and in September between 8 and 9 a.m.

The times of opening and closing given here and in the Floral Clock apply only to fine days. In cloudy, misty, and rainy weather, the flowers remain closed or only partly open; or, when these conditions are but temporary, a conspicuous retardation of opening and closing takes place, which cannot, however, be indicated numerically. Further, the observations given above relate in particular to plants well placed in regard to illumination. Such a limitation of the flowers under observation is absolutely essential, if tolerably reliable results are required. The greatest care is necessary, especially in the case of flowers which open quickly. Thus one finds with the almost suddenly-opening Gentians (*Gentiana ciliata*, *Bavarica*, and *verna*), that whilst those growing on the east or south side of a hillock have already opened wide their flowers, those a few yards away with a northerly aspect still keep their flowers closed. On luxuriant Opuntia-plants it is quite common for the flowers on the branches of the sunny side to open a long time before those on the shady side, and this with flowers of the same age.

The whole of these observations point to the fact that the opening of flowers is especially promoted by sunshine. Exactly how it is brought about, how the influence of the sun's rays in these opening-movements of flowers affects the tension of the tissues, is by no means easy of explanation. Still the question is so full of interest that it is well worth our consideration. First, we may inquire whether it is light or heat which gives the impulse to the remarkable changes in tension which lead to the movements of the petals. Plants were employed, for the solution of this question, whose flowers open directly they are reached by the first morning rays of sunshine. Specimens of *Gentiana Rhætica* and *asclepiadea* were placed in a roomy cylinder of glass in which the temperature was maintained at a low and uniform temperature. This was effected by surrounding the cylinder by a second, larger one, and causing a stream of water of a constant temperature of 7° C. to circulate in the space between the cylinders. Since this mantle of water only permitted rays of light and not of heat to pass, it would be due solely to the action of the former if the flowers under experiment opened. As the rays of the morning sun reached the cylinder the Gentians within opened their flowers. In view of this result one is justified in assuming that the opening is occasioned by the rays of light. But that it arises solely from this cause were too hasty a conclusion, as appears from the following control-experiment, conducted upon the same Gentians. They were, whilst closed, placed in a dark room over the still hot iron of a stove in a situation where the thermometer indicated 42° C. Within 3 minutes they had all completely opened.

This apparent contradiction may be explained by the assumption that the rays of light which fell upon the closed Gentian flowers in the cylinder were converted into heat. As we know, if rays of light strike any object and are not entirely reflected from its surface, they warm it (*cf.* vol. i. p. 519). This probably is the case with the Gentians, and the phenomenon may be explained as follows. The light-vibrations are communicated to the flowers and converted into vibrations of heat. This heat produces changes in the turgidity of the tissues, affecting their tension

and growth. The active energy of the heat is converted into another form of movement which ultimately alters the position of the petals, and we see the flowers opening. This explanation, further, harmonizes with the ascertained fact that under the influence of light and warmth the watery contents of certain cells in dead tissues undergo a rapid alteration, and that even in portions of flowers whose cells contain no living protoplasm changes in tension are brought about. It also agrees with the conception that the periodic opening and closing of flowers stands in relation to those chemical changes and molecular re-arrangements which we know as Respiration, Metabolism, and Growth. It has been demonstrated that flowers which exhibit periodic movements do not cease their growth on their first opening, but continue to stretch both in length and breadth. The perianth-leaves of Winter Aconites (*cf.* p. 114), Meadow Saffrons, Anemones, and Gentians, and the ligulate florets of the capitula of the Daisy, Marigold, and Leopard's Bane grow in length considerably every night. Only so long as this growth continues is an opening or closing possible, these movements cease simultaneously with growth.

The suggestion already offered as to the significance of anthocyanin (vol. i. p. 520) agrees with the idea that light is converted into heat in the tissue of the sepals. It was made probable, in the page cited, that the variously-coloured pigments known as anthocyanin possessed amongst other properties that of converting light into heat. It is particularly interesting to note that the white sepals of periodically opening and closing Anemones (*Anemone alpina, baldensis, nemorosa, sylvestris, trifolia*, &c.), show a red, violet, or blue tinge on the under side. Quite similarly coloured are the ligulate florets of many Composites (e.g. *Anacyclus officinarum, Bellis perennis, Calendula pluvialis, Hieracium Pilosella*). It is of course the under-surfaces of the sepals, petals and marginal florets of closed flowers and capitula which are alone visible. When they are closed they appear red, violet, or blue; when open, white (yellow in *Hieracium Pilosella*). The first rays of the morning sun fall first on the layers of cells coloured by anthocyanin, and we readily understand what an important part this substance may play in converting the light into heat.

Seeing that the opening of flowers and flower-buds stands to the rays of the morning sun in the relation of effect to cause, we may infer that the shutting at evening is connected with the waning light and heat. It is also to be expected that closed flowers may be made to open at will by appropriate illumination and warmth, and conversely. This at any rate holds good for a number of plants. It has been already remarked of *Gentiana nivalis* (*cf.* p. 116) that in the course of an hour, when the sun alternately shines and is obscured by clouds, it will repeatedly open and close. This is also the case with several other Gentians, with Tulips, Meadow Saffrons, and a Flax (*Linum catharticum*). In them, also, is the effect of earlier rising and later setting of the sun in northern latitudes especially conspicuous. But in the majority of flowers with periodic opening and closing, the matter is not quite so simple. True, the majority of species of Flax and Wood-sorrel, and the marginal florets of Composite heads respond to illumination and

warmth by movements, as when the sun's rays reach them in the morning after the night's rest. But when, subsequently, they have once closed it is impossible to make them open again completely the same day, vary the illumination as you will. Indeed, in the majority of these flowers the closing occurs not towards sunset, but at high noon; thus the heads of *Lampsana* and *Tragopogon* shut before the sun reaches the zenith, and several hours before the maximum temperature is attained. Then, again, there are the Dame's Violet (*Hesperis matronalis*), and many Caryophyllaceæ, which only begin to open their flowers as light and temperature wane, and shut them again ere the sun has risen. To explain these movements as being a direct consequence of illumination and warmth were as futile as to explain the sleep of man and other animals as the immediate consequence of on-coming night. Undeniably there is an indirect connection with the change from light to darkness, from warmth to cold, but conceivable only in the same manner as assimilation, metabolism and growth, in plants and animals, observe the periodicity of day and night. We may state it in this way: in different organisms certain resultant effects of assimilation, metabolism and growth become manifest at different times, the particular time depending on the advantages accruing to the organism in its special circumstances. For Man the night is the most advantageous time for sleep; for Owlet Moths and other Noctuæ it is not. For *Lampsana communis* it is of advantage in respect of its ultimate self-fertilization (to be described hereafter) that its capitula should close before noon, for the Dame's Violet and numerous Catchflies (*Silene*), that their flowers should open in the evening to receive visits from Moths (*cf.* p. 154).

These observations offer no complete or satisfactory explanation. It still remains unsolved how, in so many plants, periodic movements not depending directly upon change in the environment have become hereditary. For those who are satisfied with a fine-sounding Greek or Latin word in place of an explanation, it may be remarked that these movements of floral leaves just described have been termed *Autonomous movements*.

RECEPTION OF FLOWER-SEEKING ANIMALS AT THE ENTRANCE TO THE FLOWER.

In a volume written years ago (*Plants and their Unbidden Guests*) I divided the animals which come as guests to partake of the pollen, honey, &c., of flowers into the bidden and unbidden. The former greatly profit the plant by their visits, and there exist a multiplicity of arrangements for attracting them; the latter are unprofitable and, frequently, positively disadvantageous; when they come they must be hindered and sent away. The methods of flowers for attracting bidden guests have been already described, the reception of these and the unbidden ones at the entrance to the flower must now be considered.

And first let us see what are the arrangements which exist to enable the bidden guests to obtain the food they desire without loss of time, exertion, and, most

important of all, with advantage to the plant itself. It were a contradiction for the invited guests on their arrival to find the honey-secreting flower inaccessible, or that a flower should remain widely open when no more nourishment was to be obtained—when the meal, so to speak, was finished.

These obvious truisms apply to flowers still in bud, which it would be premature for insects to visit, and to such as have no further need of insects. It commonly happens that when a flower is pollinated its means of attraction—coloured or scented corolla—disarticulates and falls off. But cases exist in which the petals, having served this purpose, do not at once fall away, but are retained, having another part to play. When this is the case it is undesirable that they should interfere with the other younger flowers by competing with them for visitors; in a word, they must be rendered inaccessible. This is most frequently accomplished by the petals assuming the position they occupied in the bud, and often enough such a flower absolutely resembles a bud, as in the *Yucca*, represented in fig. 240[1], p. 157. Sometimes a lobe of the perianth or of the sheath-like spathe folds down, obstructing the entrance, as in many Aroids, and, in particular, in the Birthwort (*Aristolochia Clematitis*, *cf.* fig. 257[8]). In a number of cases the old flowers, which have no further need of insects, bend down out of the way of the younger ones, as may be seen in a number of Papilionaceæ and Boragineæ (*cf.* vol. i. p. 744). In *Morina Persica* and in the Brazilian Rubiacea, *Exostemma longiflorum*, the old flowers not only bend down, but undergo a peculiar change in colour, so that they are no longer noticed by insects. At the time of flowering the tubular corollas of these flowers are white and attractive to night-flying moths, being visible in the dark at some distance; but as soon as they are pollinated the corollas fade and bend down, assuming ere the following night a lurid red tinge, so that they are no longer visible in the dark.

It is similarly capable of easy demonstration that flowers provided with allurements for animals become conspicuous and accessible only at that period when visits are of real advantage. Their accessibility is then promoted as much as possible. In addition to being open the flowers are directed towards the side from which the visits of the most welcome guests are expected. In many plants, of which the Crown Imperial (*Fritillaria*), Foxglove (*Digitalis*), and *Campanula* may serve as types, the at first erect flower-stalks bend down sharply just before the opening of the flowers, so that the entrance is directed towards the ground. This position is inconvenient and unsuited to animals which would suck the honey, hovering over the flowers, to flies, accustomed to lick up honey from a flat surface, to such insects as are too timid to venture into the inside of a hollow flower, finally to beetles which require large amounts of deposited pollen. To bees and humble-bees, however, these flowers are accessible; supported by the projecting stigmas, style, and stamens, or sometimes by hairs, they easily climb up to the honey-secreting dome of the bell. Probably these insects prefer bell-shaped flowers, since here they have no competitors to fear. The ready welcome thus offered to the most industrious of all flower-visitants has this further advantage, that the desired transfer of pollen

from plant to plant is accomplished with certainty and despatch; it may be said of these hanging bell-flowers that they are directed towards the side from which the most welcome of all guests will reach them. Nor must it be forgotten that from this pendent position accrue many other advantages; thus the pollen is well protected from wet by the corolla (*cf.* p. 118), and numerous little Hymenoptera, useful in carrying pollen, use these bells as night-quarters (*cf.* p. 163).

In a large number of plants, though the closed buds are directed upwards, the

Fig. 256.—Preparation of Flowers for Insect-visits in the Laburnum (*Cytisus Laburnum*).

[1] Erect raceme; all the flowers still closed. [2] Pendent raceme; some of the flowers open.

flower-stalks bend down on opening, so that the entrance to the flower is directed sideways. When, at length, insect-visits are no further required, the older flowers collapse and point downwards. This change in the direction of the flower may be well observed in Honeysuckle (*Lonicera*), Evening Primrose (*Œnothera*), *Acanthus*, in Balsams (*Impatiens*), *Galega*, *Melilotus*, and many of the Clovers (*Trifolium*, *cf.* fig. 252[2] p. 184).

Very peculiar is the behaviour in a number of Papilionaceæ, of which the Laburnum (*Cytisus Laburnum*) may be taken as type (*cf.* fig. 256). The axis of the raceme remains erect so long as all the flowers of the inflorescence are in bud, the individual flowers being so placed that the standard is above and the keel

below (fig. 256[1]); later, the rachis becomes pendent, and the apex of the inflorescence points downwards. The buds are now so placed that the standard is below. Before the standard unfurls and the flowers become accessible, however, the stalk of each flower twists round through nearly 180°, so that the standard is again brought uppermost (*cf.* fig. 256[2]). In this position the keel is a convenient platform for visiting insects to alight upon. It is of interest to note that if the young racemes are forcibly retained in the erect position by means of strings, the twisting of the flower-stalks does not occur, or only to a very slight extent. In the nearly allied *Laburnum Alschingeri* the racemes are always borne erect, and there is no twisting of the stalks at all; by this character the two species may be readily distinguished.

Many examples of the same phenomenon are furnished by Orchids. Here, however, the twisting is accomplished not by true flower-stalks but by the stalk-like inferior ovaries. In Orchid flowers one member of the perianth, the lip or labellum, is conspicuous by its shape and size, and serves in more than two-thirds of all Orchids as a landing-stage for insects. This petal is directed upwards in the bud, and in a few Orchids always retains this position, as in the vanilla-scented *Nigritella* and in *Epipogium* (*cf.* fig. 257[10]). But in the majority of Orchids, such, for example, as grow in the meadows with erect spikes of flowers, the ovary undergoes a spiral twisting which brings the lip below so as to serve as a platform for the insects. Nor is this confined to our indigenous Orchids; it occurs also in tropical, epiphytic forms which grow perched on branches of trees or ledges of rock, when they have an upright rachis to the inflorescence; as, for instance, in *Oncidium Papilio*, one of the weirdest of all Orchid flowers, belonging to the Island of Trinidad. Many of these epiphytic Orchids, however, have not ascending but more or less pendent inflorescences; this is markedly the case in *Stanhopea*, of which a species, *Stanhopea Devoniensis*, is represented in the plate beside the *Oncidium*. Such flowers do not require to twist to bring the lip into the position in question. Indeed, in this and many other similar Orchids no twisting of the ovary takes place. If, however, a young spike of *Stanhopea* be fixed in an erect position, the flowers will all twist within twenty-four hours and take up the position which they would have occupied had the inflorescence been pendulous.

Altogether peculiar is the state of affairs in *Gongora galatea*, a tropical American Orchid sometimes introduced into European hot-houses. As in *Stanhopea*, the spikes are pendulous from the branches of old trees, but the lip of the flower in its original position below is unsuited as a platform for insects. Consequently the ovaries twist through 180°, so that the lip stands above and is of service to visiting insects.

It is an interesting circumstance that all the flowers on many erect, flowering axes turn towards the same side, so that a one-sided spike or raceme results, as in *Vicia*, *Digitalis*, *Corydalis*, and *Penstemon*. The entrance to the flowers is directed towards the side from which the visits of insects or humming-birds may be expected. When, for instance, a Foxglove (*Digitalis*) grows by the edge of a wood,

it turns all its flowers away from the shaded side where insects are not abundant, and directs them towards the sunny meadow swarming with bees and humble-bees. Some Labiates belonging to the genera *Salvia* and *Satureja* turn all their flowers one way only when they stand close to a steep wall. When they are equally exposed on all sides their flowers are directed towards all the points of the compass. A similar behaviour is observable in many plants which grow on the narrow mouldings of old, ruined walls, or on the ledges of steep rock faces, as, for instance, in the Snapdragon (*Antirrhinum majus*) and in *Haberlea rhodopensis* of the Balkans; both of these turn their flowers away from the wall or rock, even when these backgrounds are well warmed and lighted by the sun.

The visitors to laterally-directed flowers include Syrphidæ, Owlet-moths, Hawk-moths, Humming-birds—indeed all animals which suck honey whilst hovering in front of the flowers. As they require no platform, we find all flowers of this type destitute of anything of the kind.

Flowers which are visited by sun-birds (Nectariniæ), humming-birds and by night-flying moths are likewise destitute of plates, ridges, fringes, pegs, or knobs on which the animals might alight or cling. The lobes of the corolla which close the flower in bud take, on opening, a position in which they are useless as perches; indeed they bend right back so as to impede the hovering animals as little as possible as they suck up the honey with their probosces or bills. As examples may be mentioned the Honeysuckle (*Lonicera Caprifolium*), the Orchid *Habenaria bifolia* visited by Hawk-moths, and *Melianthus major* sought by small honey-drinking sun-birds (*cf.* figs. 258 [9, 10, 11, 12, 13]). When a well-developed edging or fringe is present in flowers adapted to crepuscular Lepidoptera and Humming-birds, as in *Mirabilis longiflora*, *Nicotiana affinis*, *Posoqueria fragrans*, *Narcissus poeticus*, and *Œnothera biennis*, it serves from its delicacy and position not as a platform, but, in virtue of its conspicuous white or yellow colour, as an attractive organ visible at a considerable distance in the gloaming.

Otherwise is it with flying animals which must first alight on the flower and then penetrate to the concealed honey. Like doves entering a dove-cote, they require a platform, and in point of fact such a provision is found in such laterally-directed flowers as depend on this class of visitor.

In *Epipogium aphyllum* the "column" pointing obliquely downwards forms a convenient platform for humble-bees (*Bombus lucorum*, *cf.* figs. 257 [10, 12, 13]). But on the whole the column of Orchid-flowers is rarely used in this way. Very often the stamens or style project well beyond the margin of the flower and serve this purpose, as, for instance, in the Horse Chestnut (*Æsculus*), many Liliaceæ (*Funkia*, *Anthericum*, *Paradisia*, *Phalangium*), Viper's Bugloss (*Echium*), *Dictamnus* and *Pœderota*, similarly in the large-flowered Speedwells (*Veronica*, *cf.* fig. 257 [1]). More frequently, however, the margin of the perianth or corolla is modified for this purpose. Especially noteworthy in this respect are the Aristolochias, on the flowers of which there exists an almost endless series of sometimes flattened, sometimes perch-like, alighting-platforms. In *Aristolochia ringens* (fig. 242, p. 166), it

resembles a sugar-scoop; in the Brazilian *Aristolochia labiosa* (fig. 257 [6]), there is a broad heart-shaped expansion in front of the narrow entrance to the flower; in *Aristolochia cordata* (fig. 257 [7]) there is an elongated, flagelliform perch for the flies; whilst in our own *Aristolochia Clematitis* (figs. 257 [8] and 257 [9]) there is a slightly excavated lip on which the midges can alight before entering the flower.

A multifarious variety of arrangements is met with in the perianths of Orchids and in the corollas of bi-labiate flowers for promoting access to the flowers. There

Fig. 257.—Arrangements for the reception of Insects at the entrance to the Flower.

[1] *Veronica Chamædrys.* [2] *Ophrys cornuta.* [3] *Corydalis lutea*, from the front. [4] The same, from the side. [5] *Galeopsis grandiflora.* [6] *Aristolochia labiosa.* [7] *Aristolochia cordata.* [8] *Aristolochia Clematitis*; the lowermost flower is faded and has bent down, its lip is folded over the entrance to the flower. [9] Longitudinal section of a flower of *Aristolochia Clematitis*; within the enlarged cavity of the flower are two midges (*Ceratopogon*) temporarily imprisoned by the reversed hairs of the tube. [10] Flower of *Epipogium aphyllum.* [11] Pollinia of *Epipogium.* [12] Column of *Epipogium* showing the small heart-shaped rostellum. [13] Shows the pollinia of *Epipogium* attached by their sticky rostellum to a pencil, in process of withdrawal. [9, 11, 12, 13] somewhat enlarged; the other figures natural size.

are all sorts of lobings and sinuses, fringes, pegs, and knobs on the lower lip which serve as landing-stages for alighting and as fulcrums for further explorations to numerous flies, wasps, bees, humble-bees, and butterflies. In the noble Orchid *Phalænopsis Schilleriana* (*cf.* fig. 258 [1]) the smooth and complex labellum has a little projection not far from its point of attachment which resembles, and indeed serves, as a footstool to the visiting flies. Behind the footstool is the column, the apex of which is occupied by the anther, and whose lower portion is excavated into

a stigmatic cavity. Leading into the honey-lined stigmatic cavity is a circular aperture or window, and projecting into the upper margin of this window is the little pointed, triangular rostellum like the bill of a bird (fig. 258[2]). When a fly desires to abstract honey from the stigmatic cavity, it stands on the footstool and puts its head in at the window (fig. 258[5]). In doing so it touches the extremely sticky tip of the rostellum, which sticks to the top of its head. When satisfied, the fly, in vacating the footstool, drags the two pollinia (pollen-masses), which

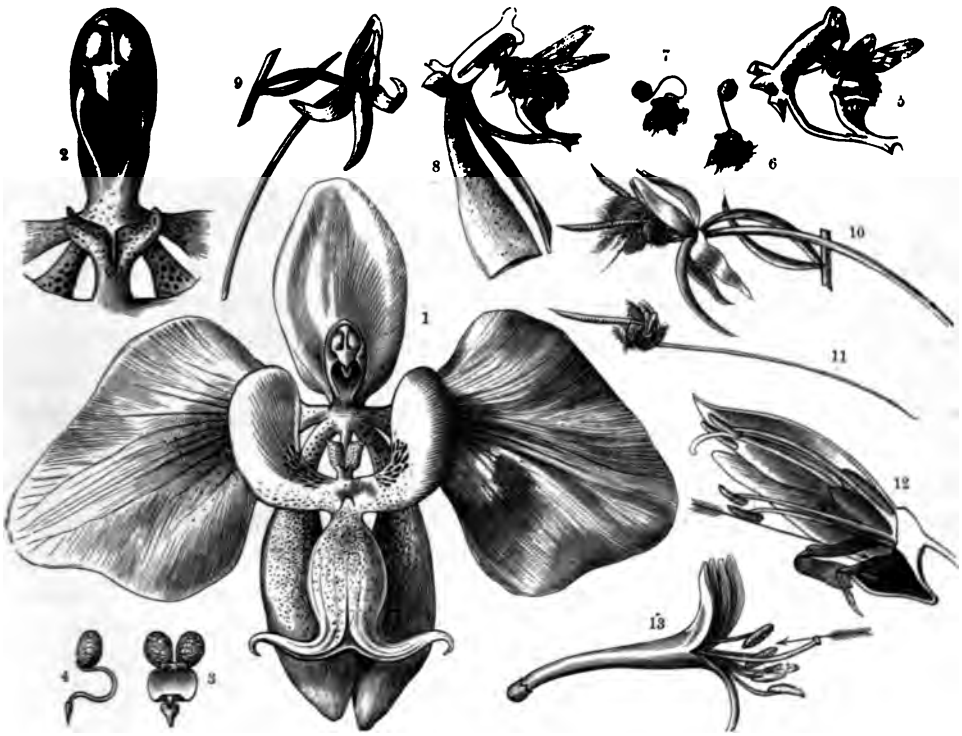

Fig. 258.—Arrangements for the reception of Insects at the entrance to the Flower.

[1] Flower of *Phalænopsis Schilleriana*. [2] Column of this *Phalænopsis*; in front of it is the little bi-lobed footstool. [3] Pollinia of *Phalænopsis* with heart-shaped gland; seen from in front. [4] The same, seen from the side. [5] A Fly which has alighted upon the footstool is introducing its head into the stigmatic cavity, and simultaneously becoming attached to the gland. [6] Head of the Fly with attached pollinia. [7] The same, the stalk of the pollinia has become bent like a swan's neck. [8] A Fly introducing the pollinia into the stigmatic cavity of another flower; the column is shown in longitudinal section. [9] Flower of *Habenaria bifolia*. [10] The same flower visited by *Sphinx pinastri*; the head of the Sphinx alone is represented, its proboscis has been introduced into the long spur. [11] Head of *Sphinx pinastri* with long proboscis. [12] Flower of *Melianthus major*, seen from the side, after removal of some of the petals. [13] Flower of *Lonicera Etrusca*. [2], [3], [4], [6], [7] slightly enlarged; the other figures natural size.

are attached to the rostellum, out of the anther, and goes away with them on its head (258[6]). It now visits another flower and again alights upon the footstool. Meanwhile the stalk of the two pollinia has bent forwards, like a swan's neck (258[7]), and as the fly puts its head in at the window the pollinia precede it into the stigmatic cavity and remain sticking to the wall (258[8]).

Remarkable, also, is the threshold provided for alighting insects on the lower lip of *Ophrys cornuta* and of the Hemp-nettle (*Galeopsis Tetrahit*). The lip of the

former has two hollow projecting pegs which give the whole flower a horned appearance (fig. 257 [2]), that of the latter two pegs, also hollow (fig. 257 [5]). In the Snapdragon (*Antirrhinum*) and in the allied Toad-flax (*Linaria*) two remarkable knobs, projecting from the lower lip, serve as a platform for insects which, by exerting pressure, force down the lower lip and gain access to the flower. It is most entertaining to observe how a Humble-bee buzzes about till it alights on the two knobs of the lower lip, and then, having opened the mouth by means of hinges on either side of the corolla, suddenly disappears into the cavity of the flower to fetch honey. In the Calceolarias the phenomenon is even more remarkable. The Humble-bee sits on the inflated, slipper-like lower lip, and opens the mouth by a light pressure against the upper lip. Then a nectary, hitherto hidden in the slipper-like cavity, comes to light, flap-like, and amply provided with honey. This nectary is presented to the Humble-bee just like a spoon as it sits on the lower lip. Directly the bee goes the lower lip snaps to, and the nectary disappears from view.

An interesting mechanism obtains in the flower of *Corydalis lutea* (*cf.* figs. 257 [3] and 257 [4]). The corolla here consists of four petals, one right and one left, one above and one below. The two latter are similar and applied together like two hollow hands. The right-hand petal is small and spoon-shaped, the left-hand one is the largest of all, and is produced outwards into a short spur which contains honey, whilst above it expands into a sort of brim. Access to the honey is obtained beneath this brim, and insects must enter here. To accomplish this the insect sits on the two median petals, which are applied together (fig. 257 [3]). But to give it a better hold, each of these petals has a median flap, which may be compared to stirrups on either side of a saddle. On these the bee gets a purchase, sitting as it were on a saddle. It may be noted here incidentally that the pollen is scattered on the under surface of the abdomen of the insect by a curious lever-mechanism; also that *Corydalis* is almost unique amongst flowers in that it is lob-sided, *i.e.* the spurred petal is not in the median plane of the flower (as in the generality of zygomorphic flowers) but is inserted laterally.

Many Papilionaceous flowers have a considerable resemblance to *Corydalis*, although their flowers are constructed on quite a different plan. The Papilionaceous flower has five petals. Of these the two front ones are united together and form the "keel", the two lateral are known as the "wings", whilst the posterior unpaired one is expanded and is known as the "standard". This standard closes the entrance to the base of the flower, where the honey is concealed, from behind so that insects seeking honey must sit either on the keel or wings. In the flowers of Sainfoin (*Onobrychis*) the wings are quite small and invisible, and here the relatively big keel serves as alighting-platform. In many others, on the other hand, *e.g.* in *Coronia*, *Orobus*, *Lotus*, and *Spartium*, the wings are folded over the keel, and meeting in the middle form a sort of cushion well suited as the alighting-place of insects.

All the flowers so far described have the peculiarity that their petals are not symmetrically arranged all round. Their right and left halves agree abso-

lutely, but the upper and under halves are quite different. In this respect they are comparable to the face of a man, to the head of a vertebrate, or to the body of an insect—indeed many of these flowers resemble the heads of animals or flies, butterflies, spiders, &c. (cf. *Oncidium Papilio* and *Stanhopea Devoniensis*, mentioned at p. 224, and *Ophrys cornuta* and *Galeopsis grandiflora*, figs. 257[2] and 257[5]). Flowers exhibiting this kind of bi-lateral symmetry are known as *Zygomorphic*. Undoubtedly this Zygomorphy of laterally-directed flowers is connected with the formation of a landing-stage suitable for particular insects to alight upon. The Zygomorphy of *Corydalis* is peculiar, as noted at the end of the last paragraph but one.

In flowers whose opening is directed upwards, quite apart from its nature, whether it be the mouth of a narrow tube or the broad edge of an expanded plate, Zygomorphy is superfluous. Such flowers are constructed symmetrically on every side. Their petals are placed like the spokes of a wheel or the rays of a star; they have been termed *Actinomorphic*.

Such flowers, directed upwards, present a landing-stage to insects either at the periphery or at the centre. Humble-bees which visit the erect, open flowers of Gentians (*Gentiana asclepiadea, pannonicæ, Pneumonanthe, punctata*) alight first on the edge of the corolla, and then climb down into the wide tube, disappearing whilst they suck the honey. In the majority of cases, however, the edge of the corolla is so extremely delicate and flimsy that heavy insects, such as beetles, would not be adequately supported, but would bend the corolla right down on to the middle of the flower. Thus, in such flowers we frequently find an expanded disc-like or star-shaped stigma which forms an admirable platform, as in the flowers of *Tulipa, Paris, Opuntia, Papaver*, and *Argemone* (*cf.* fig. 243, p. 168). In Roses, Buttercups, and Anemones a large number of carpels

Fig. 259.—Wood Anemone (*Anemone nemorosa*).

[1] Complete plant; natural size. [2] The collection of carpels from the centre of the flower; magnified.

are present in the centre forming a sort of fascicle which makes a useful platform (*cf.* fig. 259). Or, again, the style or stigma may be lobed or forked, the branches taking an oblique or horizontal position, thus resembling a perch (e.g. *Convolvulus arvensis* and *Siculus*). Or, it may be formed by the fascicled stamens in many upright, actinomorphic flowers, as in Myrtles, St. John's-Worts, the Australian Acacias and various Malvaceæ (at least in the first stage of flowering).

The Pinks and Scabiouses whose capitate flowers contain honey deep down are preferably visited by Lepidoptera, the flowers of Umbelliferæ and Euphorbiaceæ, whose honey is exposed and easy of access, by Flies, Wasps and other short-lipped Hymenoptera. To the inflorescences of Composites and Proteaceæ, the most various insects are attracted, according to the form and position of the whole inflorescence and the depth at which honey and pollen are to be obtained. It is impossible to enumerate the various cases here for lack of space, nor, indeed, would it be desirable. One more plant, *Dryandra*, one of the Proteaceæ, deserves a brief description, however, on account of the remarkable form of its inflorescence. This plant is a low shrub, a constituent of the Australian "Scrub". Its flowers are arranged around the margin of a cup about 4 centimetres in diameter. The bottom of the cup is lined with scales only, and here collect drops of liquid secreted by the flowers, which smell like sour milk. Around the margin of the cup the long styles project like pins, bent slightly inwards. The pollen is collected at the tops of the styles at the commencement of flowering; subsequently the stigmas are developed, ready to receive pollen brought by animals from other flowers. So far as is known, this arrangement of flowers and sap is not adapted to insects. It seems probable that Kangaroos visit these flowers, stick their snouts into the excavated inflorescences to drink up the sap, and unconsciously dust their mouths round with pollen which is subsequently conveyed to the stigmas. The respective heights of the *Dryandra* bushes and of Kangaroos, and the configuration of the inflorescence compared with the snout of this animal, render the assumption a not impossible one.

The efficacy of all these arrangements for promoting the quick and easy obtaining of food from flowers by "bidden guests" is obviously much enhanced by the existence of others for the exclusion of hurtful and undesired visitants. As hurtful may be characterized all such animals whose visits interfere with or prevent the speedy transfer of pollen from flower to flower. Such are small wingless animals which must of necessity reach the honey and pollen on foot. Let us consider the case of one of these little pedestrians. Suppose it to have reached a flower and covered itself with pollen; it has now before it, in order to transfer this pollen to a stigma on another plant, a long and toilsome journey beset with dangers for the pollen, quite apart from the length of time taken. The pollen may be so easily rubbed off on the journey by hairs and other structures encountered, or it may be washed off by rain. Then, even if a second flower be attained, what are the probabilities of its being in a receptive condition? How otherwise it is with the lightly-flying insects and humming-birds! They dart from plant to plant with extraordinary rapidity and visit half-a-dozen flowers within a minute or so, thus transferring the pollen

new and fresh. Winged insects and humming-birds are ideal agents for the crossing of flowers, and are the most welcomed of all guests. But even of these fleet emissaries all are not equally welcome. Of what service is it to a plant if its pollen is not deposited on the proper spot—on the stigma where it can develop pollen-tubes—be the transfer accomplished ever so quickly? Let us suppose a tiny fly entering the flower of a Foxglove. It alights on the lower lip of the corolla and makes its way to the honey at the base of the flower where the honey is, without

Fig. 200.—*Cornus florida*; numerous small, aggregated flowers surrounded by four huge bracts, which serve at once as attractive-organs and alighting-platforms for insects. (After Baillon.)

touching the stigma or stamens placed just below the upper lip. Having satisfied itself, it retreats by the same route. What advantage does the flower get from the visit of this particular insect? None. And more than this, it has been robbed of a portion of that honey on which it relied to allure some larger animal which would unintentionally stroke the anthers and stigma with its body. By the admission of small flies to Foxglove flowers consequently no transfer of pollen would be effected. Thus we see that not all flying animals are desirable visitants; that many insects, which, in consequence of their size and shape are unable to promote a transfer of pollen, must be regarded as unbidden guests, and prevented access to the honey.

Nor are arrangements such as are indicated above wanting. Peculiar folds and

cushions, walls and gratings, brushes and thickets of hairs are present, guarding the entrance and rendering access difficult, whilst still allowing it. Large and powerful animals find these obstacles no hindrance, and readily brush them aside; small ones, however, cannot do this, but have to climb over or circumvent the obstacles. And in many cases this enforced divergence by small insects from the direct path brings about the desired result. For, in circumventing these folds and barricades and hairs, they are unconsciously led past the anthers and stigmas, contact with which is unavoidable. Thus, what would otherwise be useless visitants become welcome guests. They are conducted indirectly to the honey by these curious structures, which may, in a sense, be termed "path-finders".

A more detailed consideration of these arrangements will be given when treating of the taking up of pollen by insects, in the next chapter. Mention of them cannot be omitted here owing to the difficulty of drawing an absolute distinction between contrivances designed to lead insects by a particular route into the flower, and such as entirely exclude the unbidden guests. The same difficulty obtains between the defences erected against wingless and those against winged insects, it being in many cases not easy to distinguish between them. Consequently, the grouping of these mechanisms in the sequel cannot be entirely free from the reproach of partiality; still it will serve its purpose should it render these problems more intelligible.

First of all, we will describe the mechanisms which serve to protect flowers against little wingless marauders which creep up from the ground. Remarkable amongst these is the indirect protection afforded to the floral honey by honey secreted in the region of the foliage. This may be seen in many Balsams, especially well in the Himalayan *Impatiens tricornis*. In this plant the stipules, which stand right and left at the bases of the leaves, are modified into secretory glands. Of the two glands, one is small and rudimentary, but the other extremely well-developed. The latter is a fleshy convex disc fused partly with the base of the leaf and partly with the surface of the stem, and so disposed that insects creeping up the stem must encounter it. The honey, secreted by the tissue of this gland, collects in a drop on the hemispherical and downwardly-directed cushion of this disc. Thus are the insects tempted by the way in their ascent. They find drops of honey provided for them at the base of every foliage-leaf equalling that of the flowers in quality and surpassing it in quantity; besides which it is nearer and more accessible. The honey-loving ants lick it up eagerly, and are content not to stray further upwards. Actual observation shows that the flowers of *Impatiens tricornis* are free from ants, whilst these stipular nectaries are much frequented by them. Their presence in the flowers is very undesirable, since they could readily get at the honey there without touching the pollen or stigma. And more than this; they would not only pilfer the honey, but they would also drive away those winged insects for which the honey is prepared—the welcome guests that pollinate the flowers. We are justified on the facts in regarding this diversion of the unbidden guests as an indirect protection of the floral honey.

This secretion of honey from the stipules in *Impatiens tricornis* begins just at

the time when the plant commences flowering. This must be emphasized because the suggestion has been made that the stipular secretion serves to protect the foliage indirectly from the ravages of caterpillars, snails, and beetles. The remarkable observation has been made upon several plants, for the most part tropical, that they live symbiotically with certain small and very fierce ants. The plants afford the ants lodging in special cavities and give them nourishment in the form of sugary and albuminous secretions: the ants in return defend the foliage against the attacks of leaf-eating animals. So soon as this "standing army" of ants detects the foe it commences offensive operations, like the garrison of a fortress, and by biting and squirting formic acid frightens the invader away. In this way is protected the foliage of *Acacia spadicigera* and *sphærocephala*, *Cecropia peltata*, *Clerodendron fistulosum*, *Rosa Banksiæ*, and several other plants (known as *Myrmecophilous Plants*) against the attacks of leaf-eating animals. At the conclusion of this chapter opportunity will offer to describe how the flower-buds of several Composites are similarly protected against herbivorous beetles. In the case of *Impatiens tricornis*, however, the ants are no protection for the foliage; whilst the leaves are developing, no honey is secreted and no ants are present, and later, when honey is present in plenty, and the ants are licking it up, they pay no attention, even though the adjacent leaf-blades be touched or injured.

Next to the diversion of creeping animals by means of nectaries scattered over the stem and foliage may be ranked several arrangements in which the protection afforded is of a similar indirect character. Some of these have a remarkable resemblance to the devices often employed by gardeners to shield the plants in their propagating-pits and nurseries from the ravages of snails, caterpillars, centipedes, earwigs, and other noxious insects. In order to preserve a hot-house-plant from the visits of these undesirable members of the Animal Kingdom, gardeners very frequently place the pot containing the plant in question upon another low pot inverted in a shallow dish of water; thus the plant stands, as it were, on an island, and is inaccessible to the various creeping animals indicated. Similarly in a nursery the crowns of the young trees are protected against creeping vermin by tying a sticky cloth round the stem or painting the bark with bird-lime or other sticky substance. Insects attempting to climb a tree under these circumstances become imprisoned in the girdle. Caterpillars, snails, and other animals with soft integument are often excluded by attaching belts of prickly branches to the stems.

When these expedients of the gardener are compared with many of the arrangements met with in nature for the protection especially of the honey and pollen, a remarkable similarity is at once obvious. Isolation by water, prevention of access by means of sticky secretions, rings and fringes of prickles and thorns directed so as to oppose visitors on foot—such, for the most part, are the methods employed by plants to secure immunity from would-be pilferers of their honey and pollen.

Isolation by water obtains in the case of innumerable aquatic and bog-

plants. The flowers of Water-Lilies, of which the *Victoria regia*, of the river Amazon, may serve as type, the flowers and inflorescences of the Flowering Rush (*Butomus*), of the Arrowhead (*Sagittaria*), of the Water Plantain (*Alisma*), of the Feather-foil (*Hottonia*), of Bladderwort (*Utricularia*), Villarsia (*Limnanthemum*), Frog-bit (*Hydrocharis*), Water Soldier (*Stratiotes*), and of many other plants are amply protected by the belt of water which their situation involves. Flies and beetles which come through the air for honey and pollen are welcome visitors, promoting, as they do, a crossing of the pollen; snails, centipedes, &c. are, on the other hand, kept back by the water. The basins of water formed by the bases of the leaves in the Teasel (*Dipsacus*) and *Silphium perfoliatum* (figured, vol. i. p. 239), serve a like purpose, as also do the collections of water in the funnel-like sheaths of the leaves of many Bromeliaceæ (*Æchmea, Billbergia, Lamprococcus, Tillandsia*, &c.), though this is supplemented by other advantages derived by these plants from the receptacles of water in question (*cf.* vol. i. p. 241).

More frequently even than by water the flowers obtain immunity from these visitors by *sticky secretions*. The substance formed in many cases resembles bird-lime in properties, though its chemical constitution is not fully ascertained; in others it is allied to gum-arabic, or cherry-gum; whilst in others again it is a resin or a mixture of resin and mucilage known by the name of gum-resin. Occasionally this purpose is served by latex, which readily escapes from the brittle tissues and coagulates on the surface into an adhesive substance. This last method obtains particularly in certain Asclepiads, and in many species of Lettuce (e.g. *Lactuca angustana, sativa, Scariola*). The involucral scales which inclose the flower-heads of these plants are smooth and tense, and abound in latex. No obstacle prevents creeping insects, especially ants, from climbing up to this point; but as soon as the ants reach these scales on their way to the flowers, and touch the turgid investing cell-layers, they rupture the walls of the latex-tubes (which in some cases actually project as tiny hairs on the surface) with the claws of their feet, and the milk runs out in little droplets. Their feet and abdomens are smeared with latex, and when the ant bites at the substance of the scales in self-defence its head also becomes involved in the sticky mess. It seeks to free itself of this encumbrance in a variety of ways, but the result of all these struggles is merely a further rupturing of the epidermis and discharge of latex, which adds to the embarrassment of the ant. Some of these creatures manage to escape and drop to the ground, others, not so fortunate, are glued in the coagulating latex, where their dead bodies may be seen decorating the involucre of the capitulum.

The other adhesive substances mentioned arise either from certain circumscribed cells of the flat epidermis of the stem, or else definite projecting structures known as glands, glandular hairs, capitate hairs, &c., are specialized for this purpose. In the case of flat epidermal cells, the secretion is passed out from the cells and collects between the inner and outer layers of the external wall, in other words,

under the cuticle. The cuticle is gradually raised up like a blister till it bursts and the sticky matter escapes. Such portions of the stem or flower-stalk resemble limed twigs, and might have been painted with the viscid substance. In the case of definite glands, the secretion, for the most part, diffuses through the walls to the surface, though in some cases the blister-method may obtain here also. Sometimes the secretion is freed by actual rupture of the delicate walls of the glandular cells.

Sticky secretions as protection for flowers against creeping animals occur most frequently on the flower-stalks, or on the main axis of the inflorescence. The popular names of several plants indicate at once their sticky character, as, for instance, the Catchfly (*Silene*), and the Viscid Lychnis (*Lychnis Viscaria*). So also, with their botanical names indicative of their adhesive character and of the insects caught by them, e.g. *Silene muscipula*, *Roridula muscipula*, and the specifications *viscidus*, *viscosus*, *viscosissimus*, *glutinosus*, and the like—names frequently occurring amongst the Scrophulariaceæ, Labiatæ, Caryophyllaceæ, and in the genera *Ledum*, *Cistus*, *Linum*, *Aquilegia*, and *Robinia*. That the protection afforded by these limed stems is essentially *floral* is particularly well shown in the Caryophyllaceous genera *Dianthus*, *Lychnis*, and *Silene*. The lower portion of the stem in these plants (e.g. *Dianthus viscidus*, *Lychnis Viscaria*, *Silene muscipula*) is green, and shows no trace of the sticky brown coating which is first met with below the pair of leaves subtending the flowering axes. And here it is only the upper portion of the internode, the portion in the immediate neighbourhood of the flowers that is sticky (*cf.* fig. 238, p. 154).

More frequent than a simple sticky coat is the presence of glands and glandular hairs on the flower-stalk, or on the outside of the flower itself, to which little animals climbing up the plant become adherent. Of this condition numerous examples are represented in fig. 261.

A rarely-occurring condition obtains in the flowers of *Cuphea micropetala* (fig. 262). The petals in this plant are reduced to tiny scales inserted at the top of niche-like excavations of the calyx (fig. 262[4]). The calyx is tubular and coloured, 22–28 mm. in length, and 6–7 mm. in diameter; at the base behind the ovary it is expanded into a honey-receptacle. The ovary is relatively large and obliquely placed, forming a sort of "elbow" at the point of articulation of the style which touches the upper wall of the calyx-tube (262[2]). Since the side-walls of the calyx are in close contact with the ovary, the honey-receptacle is cut off from the general cavity of the flower, as it were, by a plug. Right and left in the ovary, however, are two grooves, slightly wider in front; these form (with the calyx) two tiny canals, about half a millimetre in diameter, by which access may be had to the honey-cavity behind the ovary; usually these canals are more or less filled with honey (*cf.* figs. 262[2] and 262[3], the latter showing the orifices of the two canals and elucidating the relations of the parts). To obtain the honey, flying insects must introduce their probosces into

one of these canals. The admission of little ants to these flowers, insects useless for purposes of pollination, and likely to block up the honey-orifices for authorized visitors, would be disadvantageous. The arrangements which prevail for the exclusion of ants are so elaborate that one would think that the honey of *Cuphea micropetala* was for them quite irresistible. The mouth of the flower is rendered quite inaccessible to ants and other minute creeping insects by a fringe of tufts, each bearing a number of divergent sticky bristles (262 [1, 2, 4]). These bristles form in the aggregate a *chevaux-de-frise*, guarding the mouth of the

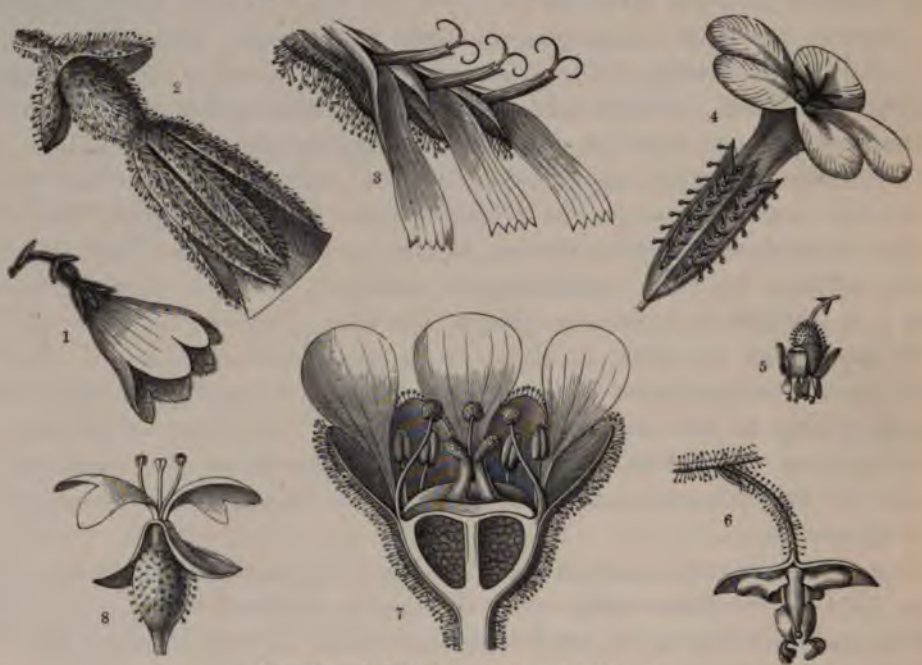

Fig. 261.—Sticky glands as a protection to Flowers.

[1] Flower of *Linnæa borealis*. [2] Calyx, inferior ovary and bracteoles of *Linnæa* (considerably enlarged). [3] Three ligulate florets from the capitulum of *Crepis paludosa* showing the glandular scales of the involucre immediately below them. [4] Flower of *Plumbago europæa*; the ribs of the calyx are provided with stalked sticky glands. [5] Flower of *Ribes Grossularia*; stalked glands shown on the inferior ovary. [6] Flower of *Epimedium alpinum*; the pedicel is glandular. [7] Section of flower of *Saxifraga controversa* with sticky glands on pedicel, ovary, and calyx. [8] Flower of *Circæa alpina* with inferior ovary covered with glands. [5] natural size; all the other figures magnified.

calyx-tube, through which these small visitors cannot penetrate. Flying insects, however, which can reach the honey hovering at the mouth of the flower, and such as can use the projecting stamens or stigma as support are not impeded by the bristles, and are, so to speak, welcomed by the flowers of *Cuphea micropetala*.

In addition to these plants, provided with adhesive glands about the flower and its accessory structures, others exist in which the whole of the foliage is sticky. As examples may be mentioned various Primulas (*Primula glutinosa, viscosa, villosa*), Saxifrages (*Saxifraga controversa* and *tridactylites*), Crassulaceæ (*Sedum villosum, Sempervivum montanum*), and several Steppe-plants (*Cleome*

ornithopodioides, Bouchea coluteoides, &c.). That their stickiness saves the flowers of these plants from many undesirable visitors there can be no doubt. Often enough the dead bodies of small creatures that have ventured upon them may be seen adhering to the foliage. In some of them the plant actually supplements its normal nutrition by a diet of these insects' bodies, and the glandular hairs would appear to subserve the same functions as the similar structures in *Drosophyllum lusitanicum,* and the various species of Sundew and Butterwort already described (*cf.* vol. i. pp. 153–156).

This is the place to mention the waxy coatings of flowering axes and pedicels, which, in a number of plants, guard the flowers from the approach of small creeping

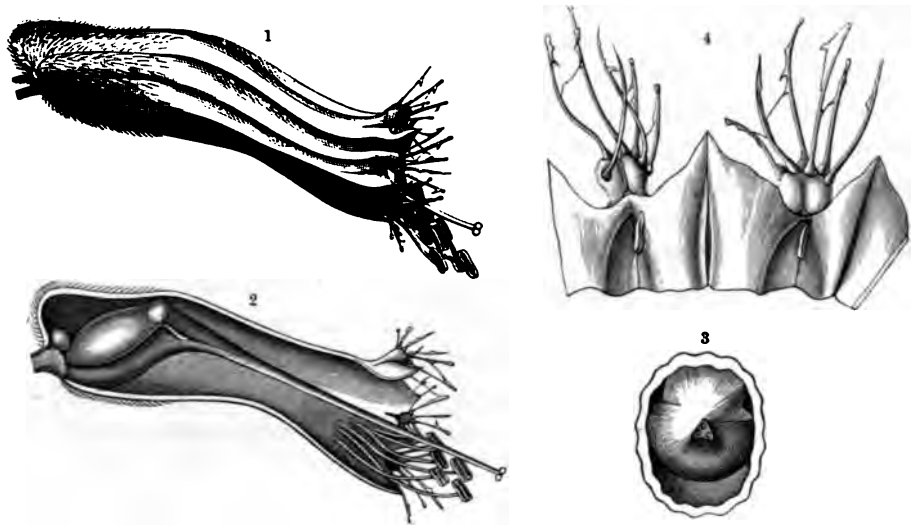

Fig. 202.—Sticky Bristles at the edge of the Calyx as a protection to Flowers.

[1] Flower of *Cuphea micropetala.* [2] Longitudinal section of the same flower. [3] Transverse section of the same flower at the height of the insertion of the style upon the ovary. [4] Small portion of the calyx-limb showing the sticky bristles in little tufts. 1, 2, 3 × 2; 4 × 8.

insects—though, of course, in many cases they serve another function. The bloom on the catkin-bearing twigs of the Violet Willow (*Salix daphnoides*) and Caspian Willow (*Salix pruinosa*) undoubtedly plays this part. For these Willows, which are dicecious and largely dependent upon bees for the transfer of their pollen, it is of importance that the honey should be reserved for useful visitors and not needlessly wasted. Ants and the like, climbing up to the catkins and attempting to traverse the wax-covered twigs, slip and lose their footing, and tumble down to the ground again.

It is not improbable, though no observations are to hand, that the stems and branches of *Melianthus, Dentaria, Sanguinaria, Fritillaria,* &c., by their slippery coating of wax provide a similar protection to the flowers which are rich in honey in each case.

It is especially hard chitinous insects, such as ants, whose progress is arrested by sticky or waxy surfaces in the neighbour[illegible] flower. Against snails and

slugs such arrangements are less efficacious. Indeed, these creatures are but little incommoded by adhesive secretions, for they can overcome any obstacles of the kind by themselves secreting a copious slime. Towards spines, prickles and stiff bristles, snails, and indeed all soft-bodied animals are extremely sensitive. Thus whilst ants and the like can travel unimpeded over the rough leaves and prickly heads of Teasels, the soft-bodied organisms avoid hispid and spinose surfaces. Stiff bristles teeth, and prickles, then, situated in the neighbourhood of the flowers, form a good protection against visitors of this class. It should be mentioned that these animals —snails and caterpillars—do not take especially honey or pollen, but devour indifferently the petals, stamens, and carpels. It is hardly necessary to describe these spiny mechanisms in detail here, as the subject has been already treated for the case of foliage (vol. i. p. 433), and the two phenomena have very much in common. Two features, however, may be pointed out as having a direct bearing on the matter in hand; firstly, where flowers as well as foliage are protected by spiny structures against creeping animals, the number of these structures increases markedly in the neighbourhood of the flowers; secondly, it often happens that spines placed immediately about the flower serve not only to exclude the unbidden guest, but at the same time as "path-finders" to direct the welcome honey-sucking insect, so that it shall dislodge the pollen and disturb the stigma.

This latter feature applies in marked degree to the sheathing bract-like investments of many flowers which must be surmounted by insects before they can reach the honey. The small capitate flowers of Composites, Scabiouses, and many Pinks are very rich in honey; but this honey is only for insects which visit the flower from above, where the stamens and stigmas are displayed. The illegitimate removal of honey—from below or from the side—must be prevented. Now many insects, especially bees and humble-bees, when they come across honey inclosed in a delicate sheath bite through the wall and steal the honey, as it were, through a back-door. Liability to this class of pilfering must be excluded by tough, impenetrable sheathing structures around the basal, honey-containing regions of the flower. Such structures are well shown on the Teasel-heads and capitula of many Pinks, in which the nectariferous portions of the flowers are protected by imbricating scales. The strongest humble-bee cannot pierce them, and the only alternative is to obtain the honey in the legitimate manner.

It is very generally assumed, and in several cases on adequate grounds, that the inflated calyces and sheaths of bracts which inclose the flowers of many plants serve to protect the honey from marauding of the kind indicated. Thus, in a case in which the honey is distant 20 millimetres from the wall of an inflated calyx, it cannot be reached by the humble-bee whose proboscis is only 8 millimetres long by means of a hole bitten in the calyx. Humble-bees will visit the flower by the ordinary way and get the honey thus with less expenditure of energy. But such relations do not generally obtain; in a majority of cases the interval between the inflated calyx, and the honey is less than 8 millimetres, so that the average humble-bee could get the honey by biting

through. As a matter of fact, however, it is usually easier for the bee to get the honey in the ordinary way, and these arrangements of inflated calyces are rather of the nature of protections against creeping insects, ants, and the like than humble-bees. There are in the European Flora some 300 plants whose flowers are robbed by humble-bees biting through the calyx or corolla. For several of them, which depend entirely upon insects for the transfer of their pollen, this burglarious proceeding is fatal. Fertilization is not accomplished; their ovules atrophy and propagation by seed is impossible. Such plants have flowered in vain. Herein lies a contradiction to the otherwise marvellous harmony which exists between the configuration of plants and animals, a contradiction only explicable on the assumption that these plants, whose honey is taken without concurrent pollination, date back to a time at which humble-bees were absent from the district in question. A Catchfly (*Silene Pumilio*), the flowers of which are industriously visited by humble-bees, occurs in the Eastern Alps (Taurus). The great majority of these bees decline to enter the flowers properly, but, hanging on to the inflated calyx, bite a hole in it and take the honey. The Catchfly rarely sets seeds, and one may see hundreds of plants together, not one of which has ripened a fruit, although they flowered freely during the summer. At the present time this Catchfly has a very restricted distribution in the Alps, and even in districts where it occurs is sporadic. Nor does it propagate with any vitality. The same is the case with another Catchfly (*Silene Elizabethæ*, of the Southern Alps) and with several species of Aconite and Corydalis. Any one familiar with the facts, although he may not be an enthusiastic supporter of current hypotheses as to the history of the vegetable world, must admit:—(1) That these endemic species are becoming extinct in the Alps. (2) That the humble-bees are to blame for this in that they steal the honey without doing the plants any service in return. (3) That these plants date back to a time at which humble-bees did not frequent the regions where they grow, and at which the flowers needed protection only from creeping insects.

The bulk of the arrangements, so far described for the exclusion of unbidden guests, occur outside the cavity of the flower, and are directed against creeping animals which climb up from the ground. Those, on the other hand, directed against undesirable winged-insects are situated chiefly *inside* the flower and take the form of hairs and fringes. These may be arranged either into irregular tufts and woolly plugs, or with greater regularity, into lattice-works, cages, and crowns of hairs. Thus we find a woolly thicket occupying the whole cavity of many bell-shaped and urceolate corollas, as in the Bearberries (*Arctostaphylos alpina* and *Uva-ursi*, fig. 263 [1]), or the hairs are confined to the tubular portion of the corolla as in the little alpine *Primula minima*. In the Alpine Roses (*Rhododendron hirsutum* and *ferrugineum*) and in several of the Honeysuckles (*Lonicera nigra*, *Xylosteum*, and *alpigena*, fig. 263 [7]), the stamen-filaments and parts of the corolla contribute hairs, which, in the aggregate, make a thicket defending the honey. Often the corolla is quite smooth inside, and the bases of the stamens alone are provided with flocks of hair which screen the nectaries, as in *Atropa*, *Lycium*, and *Polemonium*. In the well-

known climber *Cobæa scandens*, the insertion of each stamen is inclosed in a regular felt, and these five felty tufts form, as it were, a sort of diaphragm which cuts off the honey-secreting, basal region of the flower from the main cavity of the bell (see fig. 263 [5]). Again, in the Tulip (fig. 263 [4]), each stamen secretes honey at its

Fig. 263.—Tufts of Hair as a Protection to Flowers.

[1] Longitudinal section of the flower of the Bearberry (*Arctostaphylos Uva-ursi*). [2] Longitudinal section of flower of Red Valerian (*Centranthus ruber*). [3] Transverse section of the same flower. [4] Portion of the flower of *Tulipa sylvestris*. [5] Longitudinal section of flower of *Cobæa scandens*. [6] Longitudinal section of flower of *Daphne Blagayana*. [7] Longitudinal section of flower of *Lonicera alpigena*. [8] Longitudinal section of flower of *Vinca herbacea*. [9] Single stamen of *Vinca*. [10] Style and stigma of *Vinca*. [5] Natural size. All the other figs. magnified.

base in a little depression of the filament on the side directed towards the perianth. Tufted hairs completely cover the nectary, so that insects have to lift the whole stamen to get honey. In *Daphne Blagayana* (fig. 263 [6]) the stalked ovary is enveloped in hairs, by which the honey formed at the base of the flower is protected from unbidden guests.

In the flowers of *Vinca herbacea*, indigenous to the Steppes of the Black Sea (*cf.* figs. 263 [8, 9, 10]), the apices of both stamens and stigma are provided with tufts of hairs which interlock and close the mouth of the corolla-tube, as it were, with a plug of cotton-wool. One of the most curious of these arrangements is found in the Red Valerian (*Centranthus ruber*, fig. 263 [2]). The corolla-tube is some 12 millimetres long and scarcely 1 millimetre in diameter; it is divided longitudinally by a membraneous diaphragm into two tubes, of which the upper contains the long style, whilst the lower one, produced into a spur, contains the honey. This lower tube is lined throughout its entire length with hairs, which, although they present no obstacle to the introduction of a proboscis, prevent little insects from creeping in and stealing the honey. As may be seen in fig. 263 [3], these hairs project a considerable distance into the interior of the tube.

Hedges or palisades of erect elastic hairs or fringes, inserted on circular cushions in tubular corollas, are not infrequently met with. These fringes stand straight out into the tube and conceal its cavity. They are sometimes quite at the mouth of the tube, as in *Veronica officinalis*, sometimes a little distance down the throat, as in the Vervain (*Verbena officinalis*), or quite at the base, as in *Acanthus*, *Phlox*, *Horminum*, and *Prunella*. Fringed scales in rings are found in the flowers of many Genetians and Passion-flowers. In several Rutaceæ, *Haplophyllum*, for instance, hairs from the bases of the stamens form a sort of lattice-work at the base of the flower, whilst, in a species of *Monotropa*, the cushion beneath the stigma bears radiating hairs which, reaching as far as the corolla, make an elegant grating. The honey in *Swertia perennis* is secreted in little cup-like depressions near the bases of the petals. The margins of the cups are fringed with hairs which converge, and are so interwoven that the cups are protected by little cages. These few examples are typical of a vast series of lattices, gratings, and the like, occurring in flowers to shield the honey.

Protection from undesirable visitors is also obtained in a great variety of ways by the bending, twisting, or convergence of various parts of the flower, so that the honey is hidden in grooves and special cavities. Amongst these are included flowers with long, narrow tubes, into which the delicate proboscis of a butterfly can be introduced, but which are too narrow for small insects to crawl into; also, such as have various projections, cushions, and lobes of the corolla which narrow or subdivide the aperture; finally, closed flowers which can only be opened by powerful insects, and such as have their stamens so crowded that little insects cannot obtain access to the honey. Several of these have been already described and figured (p. 180, 181).

We may also regard the periodic display of attractions to insects as being, in a way, of the nature of a protection against unbidden guests. The subject has been already alluded to (p. 156) in detail, so we need only add that the arrangements obtaining in many moth-visited Caryophyllaceæ are also found in *Zaluzianskia lychnidea*, a Scrophularineous plant from the Cape. Its flowers have a long honey-secreting tube and spreading limb (as in *Silene*), the ten lobes of which are dark

purple underneath and brilliant white above. By day the lobes are furled, so that their dark inconspicuous sides are shown, nor is there any scent or other attraction; consequently it remains unnoticed by day-flying insects. But in the evening the lobes of the corolla fold back, and the white flowers are now conspicuous, whilst a strong Ylang perfume is given off to attract moths. In *Hesperis tristis*, *Pelargonium atrum* and *triste*, there is a similar periodic exhalation of perfume, though the inconspicuous petals always remain in one position. But here the scent is the main attraction, and at nightfall numerous moths are attracted by the delicious

Fig. 264.—Capitula of *Serratula lycopifolia* protected by Ants (*Formica exsecta*) from the attacks of a Beetle (*Oxythyrea funesta*).

perfume of Hyacinths which is then apparent. *Hesperis* is visited by great numbers of Owlet-moths (Noctuæ) of the genus *Plusia*, which transfer the pollen from flower to flower.

Silene nutans, already so fully described (p. 154), may be regarded as the type of the plants now under consideration. It is additionally interesting in that it possesses a double protection against unbidden guests. By its unattractive character during the daytime it is protected from diurnal flying insects, whilst the sticky secretion on its flowering axis keeps off crawling animals such as ants.

So much has been said in this chapter concerning ants as undesirable visitors, and of the means for their exclusion, that this is an appropriate place for a brief account of certain instances in which they are of real service in guarding and

protecting flowers. We have already seen how ants are diverted from visiting flowers by honey secreted on the foliage, and how, in certain instances, an actual symbiosis obtains between the plant and the ants. Especially do these ants protect the foliage from the attacks of leaf-eating animals. This reciprocal service, performed by the ants, is in no wise of the nature of gratuitous philanthropy, it is done in their own interests. The lodging and the food which the ants obtain from the plant constitute two of their most important necessities, consequently it is worth their while to protect the "goose that lays the golden eggs".

A similar state of affairs is met with on the capitula of several Composites indigenous to South-eastern Europe, e.g. *Centaurea alpina* and *Ruthenica*, *Jurinea mollis*, and *Serratula lycopifolia*—the last of which is figured opposite. The young capitula of these Composites are particularly liable to the attacks of devouring beetles, especially of *Oxythyrea funesta*, which bites big holes in the heads, destroying crowded flower-buds and involucral scales without the least difficulty. To meet this danger a garrison of warlike ants is employed. Honey is secreted from big stomata on the imbricating scales of the still-closed capitula in such quantities that one can see a drop of it on every scale in the early morning, whilst later in the day, as the water evaporates, little masses, or even crystals of sugar are to be found. This sugar, either in its liquid or solid form, is very palatable to the ants, which habitually resort to these capitula during the period of its secretion. And to preserve it for themselves they resent any invasion from outside. If one of the aforementioned beetles appears they assume a menacing attitude. They hold on to the involucral scales with their last pair of legs and present their fore-legs, abdomen, and powerful jaws to the enemy, as shown in fig. 264. Thus they remain till the beetle withdraws, if necessary hastening its retreat by squirting formic acid in its direction. Then they quietly begin to feed on the honey again. Ants of the same species do not fight amongst themselves on these Composites, although as many as ten to fifteen specimens of the ant *Camponotus Æthiops* live on each capitulum of *Jurinea mollis*, and about the same number of *Formica exsecta* on the heads of *Serratula lycopifolia*.

As soon as the florets on the heads begin to open, the secretion of honey diminishes and ultimately ceases. No longer do beetles come to devour them, nor is there any further need for protection. The garrison is withdrawn, the ants going away in search of other, younger flower-heads.

TAKING UP OF POLLEN BY INSECTS.

Having obtained in the last chapter a general survey of the contrivances in connection with the advent and reception of insects at the portals of flowers, we are now in a position to describe the means whereby insects, after reaching the flowers, are covered with the pollen there awaiting them.

The simplest case is that where the insects rove and climb about the flowers, and so get powdered all over with pollen. This happens in innumerable Umbelli-

feræ, Dipsaceæ, and Caryophyllaceæ, which, owing to the association of large numbers of flowers in umbels, fascicles, spikes, or capitula, afford a playground richly furnished with slender waving stamens where pollen is easily to be shaken or brushed off the anthers on every hand, although each single blossom only contains a few stamens. In the case, too, of the single flowers of Roses, Anemones, Peonies, Poppies, Magnolias and Opuntias, which are well supplied with stamens, insects pushing between the anthers or feasting on pollen that has dropped upon the petals get covered on head, thorax, abdomen, wings, and legs with the floury pollen. This is true also of the spathes of Aroideæ and of fig-inflorescences which are haunted by midges, beetles, and gall-wasps, and deposit their pollen on these visitors as they crawl out of their temporary refuge in the manner described on pages 156–160. Mention was made in the same chapter of the fact that insects, after being imprisoned for a time in the flowers of the *Aristolochia*, are quite covered with pollen when they emerge. The phenomenon, which was there merely glanced at, is so remarkable that it is worth while to give a somewhat fuller account of it. In the widely-distributed species of Birthwort represented in fig. 257 [8] on p. 226, and named *Aristolochia Clematitis*, the way into the enlarged base of the flower is over a convenient ligulate alighting-place and through a dark and comparatively narrow passage lined with hairs. The free extremities of these hairs point inwards, *i.e.* towards the inflated chamber, and they permit visitors from the insect-world—small black midges of the genera *Ceratopogon* and *Chironomus*—to pass into the chamber. But once inside, the midges are obliged to reconcile themselves to remaining imprisoned for a couple of days. The hairs, whilst offering no hindrance to ingress present a bristling stockade of points to insects seeking to escape (see fig. 257 [9]). At first the midges endure their captivity with complacence, for the warmth of their dungeon suits them, whilst the succulent cells lining its walls afford a certain amount of nutriment. On the second or third day of imprisonment the lateral walls of the anthers, which are adnate to the stigmatic column, open and let the mealy pollen fall to the bottom of the chamber. The pollen is also acceptable to the midges for food, and they feast upon it liberally. At last, however, they become restless and look for a means of exit, and in bustling actively about the chamber, they cover their entire bodies with pollen. After this the hour of their deliverance is no longer deferred. The hairs in the narrow passage wither and collapse, leaving a free exit, and the midges all be-powdered with pollen hasten to leave the flowers. That they retain no unpleasant recollection of their temporary confinement may be inferred from the fact that they have no sooner escaped from one flower than they creep into another, which has only just reached the stage at which entrance becomes possible. This latter circumstance must be emphasized in order to arrive at a complete understanding of the significance of the curious phenomenon just described. The moment the flower is accessible to insects, the stigma is ready to receive the pollen whilst the anthers are still closed. When the midges proceed from an older to a younger flower, they brush against the latter's stigma, which is situated right in front of the inner end of the dark passage, and deposit

the pollen they have brought with them upon it, and may thus bring about cross-pollination between the different flowers.

In many cases insects visiting the interiors of flowers only get smeared with pollen on the upper or the under parts of their bodies, or at particular spots merely, and the adherence of the pollen ensues on their rubbing against the anthers which are situated along the insect's route when it enters or leaves the flower. This process takes place in a great variety of ways. In one case, the only part dusted with pollen is the proboscis; in another, the head; in a third, the shoulders or back; in a fourth, the upper surface of the abdomen; in a fifth, the under surface of the abdomen. There are instances also in which the pollen is only brushed off by the peculiar collecting-brushes on the legs of bees which were spoken of in the last chapter. Again, reference was made on page 153 to the remarkable case of the small moth *Pronuba yuccasella*, which has the first joint of its maxillary palp metamorphosed into an organ of seizure, and by means of that implement collects the pollen from *Yucca*-flowers, makes it up into a ball and holds it fast in front of its body (see fig. 240 [5], p. 157).

If stamens, projecting out of the flower or situated on the floral threshold, serve as a place for insects to alight on, as, for instance, in the flowers of Funkia, Viper's Bugloss, Figwort and Monkshood (*Funkia, Echium, Scrophularia, Aconitum*), pollen adheres to the underneath part of the insect's body the moment it settles, or as it crawls towards the interior of the flower. In one of the species of Alpine Rose (*Rhododendron Chamæcistus*) and in the Germander Speedwell (*Veronica Chamædrys*; see fig. 257 [1], p. 226), insects visiting the flowers, which are directed laterally, grasp the exserted stamens with their front legs as if they were perches. The stamens are arranged so as to bend downwards and inwards when touched, thus they become almost instantaneously applied to the under surface of the insect's body, which becomes smeared with the pollen. Great quantities of pollen adhere to the under parts of insects in the case of Composite inflorescences. Shortly after the opening of the corollas, the style bearing an external load of pollen is exserted from each of the little tubular and ligulate florets composing the capitulum in this group, and, owing to the fact that large numbers of these florets invariably open simultaneously, numbers of styles laden with pollen project close together from the discoid head. A largish insect settling on a capitulum may therefore be dusted with the pollen of numerous florets at once. As he twists and turns about on the disc of the inflorescence inserting his proboscis into one floret after another a lot more pollen is brushed off on to the under surface of his body, and he finally leaves the capitulum with an abundant freight.

The transference of pollen to insects takes place in the Lady's Slipper Orchid (*Cypripedium*) in a manner altogether peculiar. Here it is only one of the shoulders of the visitor that receives the pollen. We will briefly describe how this happens in the case of the European species (*Cypripedium Calceolus*). The floral envelope of this Orchid (see fig. 267 [1]) consists of six leaves, one of which is shaped like a slipper, and has its deep cavity furnished at the bottom with hairs full of

sap. Sometimes little drops of nectar are also secreted by the cells composing these hairs. Certain small bees of the genus *Andrena* are in the habit of entering the cavity to feast on the hairs. Three ways are open to them, viz. the two small orifices in the background on either side of, and close to, the column, and the large oval opening in the middle of the slipper and in front of the column. They choose the last and slip under the broad, rough stigma to the bottom of the slipper where they feed on the succulent cells of the hairs. After a time they wish to escape into the open air again, but that is not so easy. The edges of the large central opening are inflected (see fig. 267 [2]), and so fashioned as to be unscalable, and the bees have no choice but to make use of one of the two little exits at the back of the slipper.

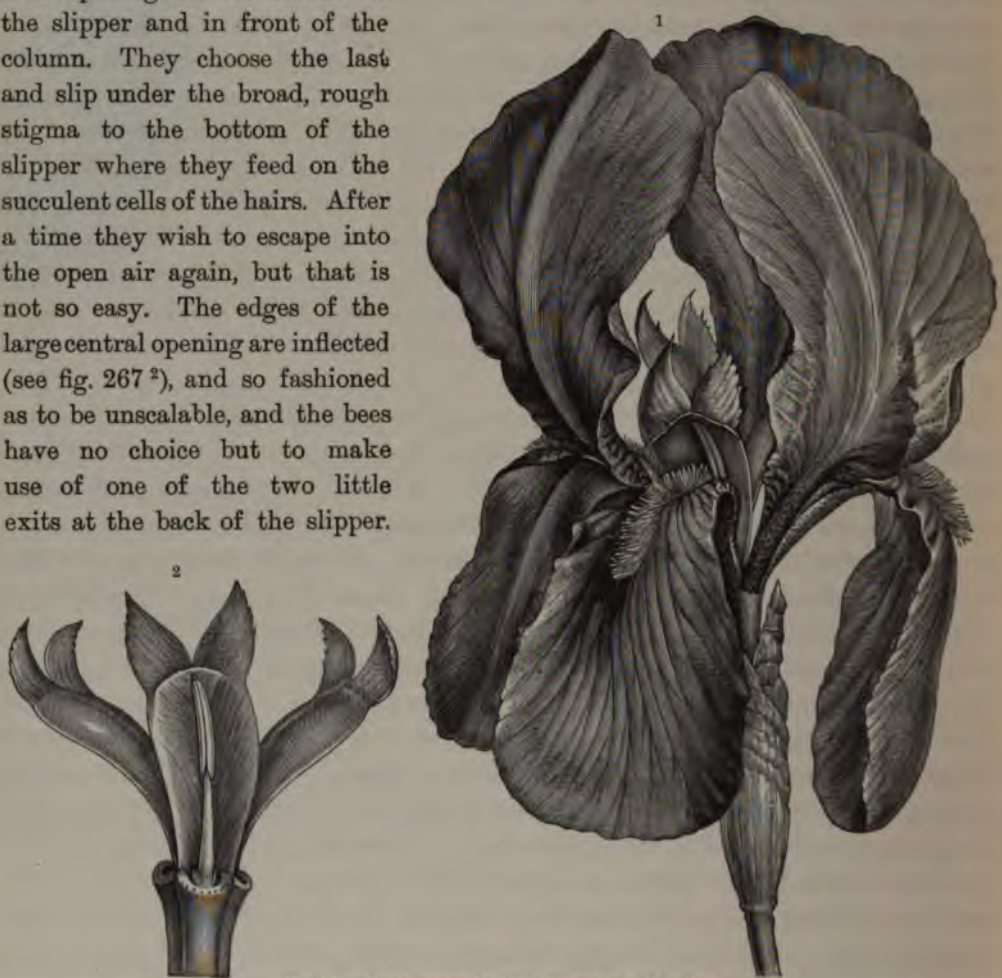

Fig. 265.—Contrivances for loading insects with pollen.

[1] Flower of an Iris (*Iris Germanica*), with three segments of the perianth reflexed and three erect. On each of the former is a strip of yellow hairs which stand out conspicuously from the violet background of the perianth-segment, and serves as a guide to insects entering the honey-containing tube of the perianth. [2] Upper half of the perianth-tube showing the three passages leading to the honey. Above each passage is a stamen with a long, linear anther facing outwards, and arching over each stamen is one of the three bi-lobed petaloid stigmas. The perianth-lobes have been removed.

Even through these escape is not altogether easy, the bees being obliged to squeeze through the narrow opening. The result is that one shoulder brushes against the soft, viscid pollen of the anther which forms the inner border of the orifice. The last act in the story is the entrance of the insect with its shoulder covered with pollen into another *Cypripedium* flower, whose rough stigma is thereupon immediately besmeared with pollen.

Instances are very common in which insects in seeking honey brush the upper parts of their bodies against the anthers, thus covering their backs with pollen. Humble-bees, when they visit Iris flowers (fig. 265), settle on the hairy ridges of the outer deflexed perianth-segments as the most convenient alighting-places, and thence proceed to the honey-containing canals of the perianth-tube. They thus pass under one of the petaloid stigmas, and at the same time under the corresponding stamen, which is so placed and curved as to exactly fit the dorsal surface of the humble-bee. The pollen is thus brushed off on to the insect's back. Similarly, bees entering the gaping flowers of *Gladiolus*, of the Dead Nettle (*Lamium*) and other Labiates rub their backs against the anthers, which are concealed close underneath the upper lips, and carry away pollen on that part of their bodies only. The same holds good in the case of the humble-bees which slip into the large bells of Gloxinia, clamber up to the honey in Foxglove flowers (*Digitalis*), or venture into the jaws of

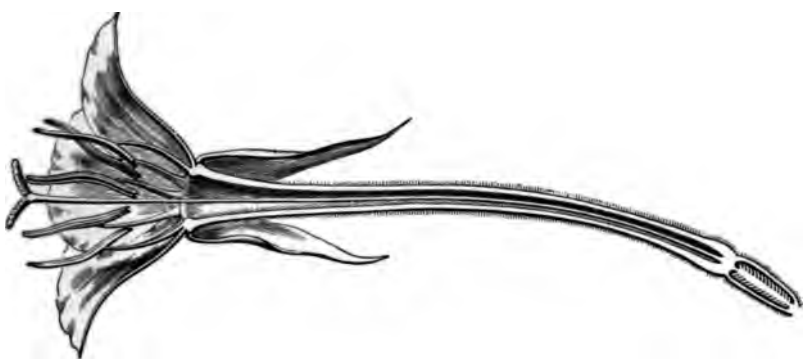

Fig. 266.—Longitudinal section through a flower of the Evening Primrose (*Œnothera biennis*).

the Snapdragon or Toad-flax (*Antirrhinum, Linaria*). In the flowers of *Linaria* two pairs of large anthers are situated close under the arch of the upper lip, and the pollen discharged by them is in the form of two round balls, which are both detached at once from the fissures in the anthers upon the occasion of an insect's visit, and are carried away to other flowers on the back of the intruder.

The laterally-directed flowers of the Evening Primrose (*Œnothera*; see fig. 266) are visited by moths which insert their probosces into the long floral tubes as they flutter about in front of the flowers. In so doing, the moths brush their heads against the anthers surrounding the entrance to the flower-tubes, and cover them with pollen. The head is also the part affected in the case of the Sun-birds (*Cinnyridæ*) which take the rich brown honey from the lower, bowl-shaped sepal of *Melianthus* flowers (see fig. 258 [12], p. 227), and in the process bring their heads into contact with the anthers above it.

The adaptation of flowers with a view to ensuring that insects seeking their honey shall brush off the pollen with some part of their bodies, whether back, belly, shoulders, head, or at least the proboscis, is of so manifold a character that it is impossible, having regard to the scope of the present work, to deal with all the contrivances coming under this category. Only a few of the most striking

examples will be described, and as they are to a certain extent identical with those already referred to in connection with the subject of the protection of honey, we need not enter into them at so great length as would otherwise be necessary. In the first place, there are the flowers which are furnished inside with prickles or sharp, stiff bristles. It is well known that honey-sucking insects, such as humble-bees, are very careful of their probosces, keeping them in special grooves in their bodies whenever they are not in use, and taking pains when they do use them not to thrust them against rigid points on account of their liability to injury. Thus a flower, furnished with sharp prickles or bristles, only admits an insect's proboscis by a well-defined path. The intruder avoids the points, and is thereby prevented from entering by a route which would not involve its rubbing against the anthers —and is induced to take a course inevitably accompanied by the deposition of pollen on its back, head, or proboscis. This occurs, for instance, in some Cruciferæ (*Braya alpina, Malcolmia Africana*; see fig. 267 [6]), where the insects are guided to the honey between two series of rigid upright bristles borne by the ovary, and are obliged to brush their heads and probosces against the pollen-laden anthers. The same thing happens in *Leonurus heterophyllus* (see fig. 267 [7]), a Labiate, which has a patch of sharp prickles in the throat just behind the under-lip. Insects desirous of possessing the honey secreted at the base of the flower, and at the same time of avoiding the prickles, are obliged to insert their probosces close under the upper-lip, and are thus brought into contact with the pollen-covered anthers there situated. In several small alpine Gentians, such as *Gentiana glacialis* and *G. nana*, the entrance to the interior of the flower is covered by four valves with lacerated margins which are so pliable as to form no barrier to the entrance of the stronger kinds of insect. But no anthers would be brushed by their probosces if they were to enter by that way, and the possibility of such an occurrence must, therefore, be obviated. The fringed edges of the valves closing the throat are for this purpose thickly studded with minute prickles. Insects reject the route as too risky and prefer to enter between the points of insertion of the valves whence passages of adequate size and quite free from danger lead to the honey. In passing along them the insects brush the anthers which are situated close by. The compulsory condition imposed on insect-visitors that they should rub the pollen off with their probosces, and occasionally with the tops of their heads and front parts of their thoraces, depends in many cases on the fact that there is only one approach leading to the honey, and the external orifice of this passage is straitened by a ring-like callosity, or by the presence of flaps or scales, whilst the anthers are situated round the orifice, or just underneath it. This arrangement is found, for example, in many Boragineæ, Oleaceæ, Primulaceæ, and Polemoniaceæ. The hawk-moth, which sucks honey in the autumn from the flowers of the Phlox, a plant belonging to the Polemoniaceæ, and butterflies, which feast in the spring on the sweet juices of Lilac-flowers load only their probosces with pollen, for, in consequence of the form and disposition of the various parts of the flowers, this part alone comes into contact with the anthers.

The same mechanism exists in so-called "revolver-flowers," *i.e.* flowers which exhibit within their outer portals the open ends of a number of small tubes resembling the barrels of a revolver. These tubes are arranged in a great variety of ways. In Bindweeds and Gentians (*Convolvulus, Gentiana*) the filaments are adnate to the corolla-tube and project in the form of ridges towards the central ovary, and so divide the main tube into four or five separate pipes. In some Geraniums and several species of Flax (e.g. *Geranium Robertianum, Linum viscosum*), a ridge arises from the middle of each petal and projects towards the centre of the corolla,

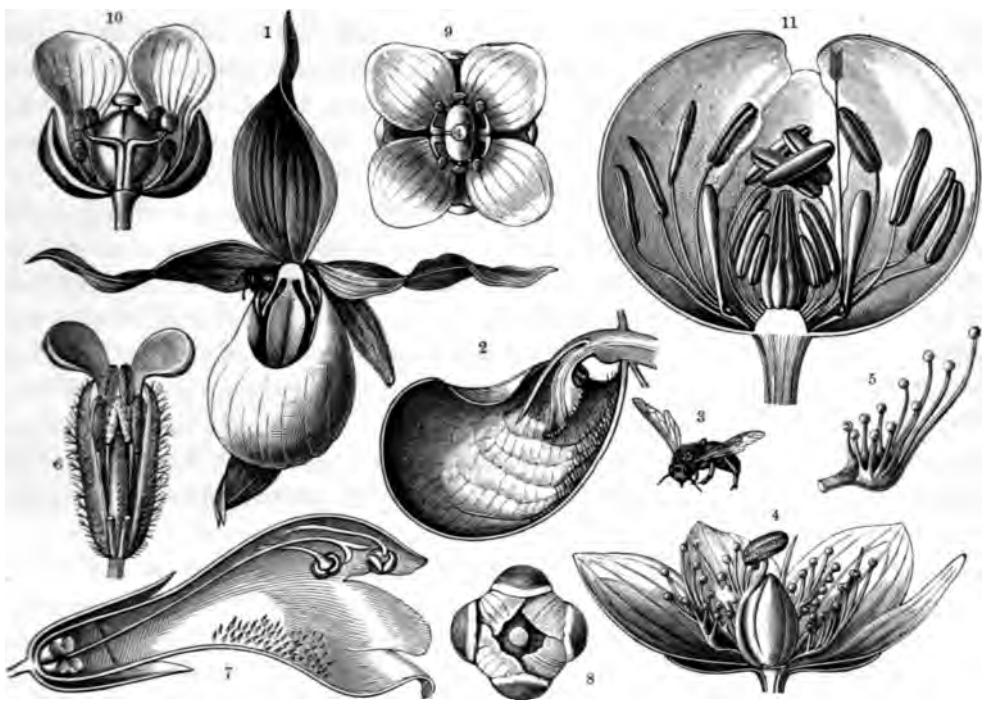

Fig. 267.—Contrivances for ensuring the deposition of pollen on insect-visitors.

[1] Flower of the European species of Lady's Slipper (*Cypripedium Calceolus*). A bee (*Andrena*) is forcing its way out through one of the holes at the side of the stigma and smearing its shoulder with pollen. [2] Longitudinal section through the labellum and column of the Lady's Slipper. [3] An *Andrena* on the wing. [4] Flower of Grass of Parnassus (*Parnassia palustris*) with the front sepals, petals, nectaries, and stamens cut away; of the stamens which are visible three are despoiled of their anthers, the fourth has assumed a position placing the anther in the middle of the flower. [5] Single nectariferous scale from the flower of *Parnassia*. [6] Flower of *Malcolmia maritima* with the front sepal, the two front petals, and two stamens cut away; the visible portion of the ovary bearing a longitudinal row of stiff bristles (white). [7] Longitudinal section through the flower of *Leonurus heterophyllus*. [8] Flower of *Kernera saxatilis* in the first stage of development, seen from above. [9] The same at a later stage of development, seen from above. [10] The same flower, seen from the side, with the front sepal and the two front petals removed. [11] Vertical section through a flower of *Trollius Europæus* (Globe-flower). [1] and [2] nat. size; the rest × 2-3.

dividing it into five tubes, which surround the styles and stamens in a circle. In Flaxes of the group *Cathartolinum* each petal is swollen in the middle and attenuated, and concave near the edges; the juncture of the concave margins of adjacent petals gives rise to a flat canal which leads to the floral receptacle. The corolla-tube of the Winter Cherry (*Physalis*) is fluted by five grooves, which, together with the villous filaments facing them, form as many tubes. In all these

"revolver-flowers" the anthers are so placed with their pollen-covered faces in front of the mouths of the tubes, that insects inserting their probosces are bound to rub against them.

The flowers of the Wild Mustard (*Sinapis arvensis*), *Diplotaxis*, and several other Cruciferous plants have anthers, which, after dehiscence, execute spiral twistings with the object of turning the face covered with pollen away from the stigma, and placing it near the spot where insects insert their probosces for the honey. In other Cruciferæ, with flowers somewhat resembling "revolver-flowers" in structure, although the approach to the honey is not straight through a tube, the stamens exhibit characteristic bendings of the filaments with a view to bringing the anthers into the line of entrance to the nectar. Thus, for instance, in the flowers of *Kernera saxatilis* (see figs. 267 [8, 9, 10]), honey is only to be found on the two narrow sides of the compressed ovary, although there are petals all round the ovary. Supposing all the filiform filaments, whether in front of the narrow or of the broad sides of the ovary grew straight up, only the anthers borne on the former would deposit their pollen on the honey-sucking insects. In order to render the anthers situated opposite either of the broad sides of the ovary which are destitute of honey liable to be stroked by intruding insects, their filaments are bent at right angles, as is shown in figs. 267 [9] and 267 [10]. By this means all the dehiscent anthers of the flower are brought into such a position as to be necessarily rubbed by insects when they come to suck the honey. Movements of stamens, directed to the same end, are also observed in numerous Caryophyllaceæ, Ranunculaceæ, Saxifrageæ, Crassulaceæ, and Droseraceæ. The floral structure in the Caryophyllaceous plants coming under this category is similar to that of "revolver-flowers"; the petals are unguiculate, that is to say, they are composed of an inferior very narrow part inserted in the tubular calyx, called the claw or *unguis*, and a flat expanded region above the calyx called the *lamina*. A groove runs down the middle of the claw to the floral receptacle, and at the upper end of the groove, where butterflies are to introduce their probosces, the lamina is sprinkled with bright-coloured patches or speckles, and is furnished sometimes with scales arranged in pairs, or something else of the kind to make the entrance conspicuous, and regulate and facilitate the introduction of the proboscis. In these Caryophyllaceæ the anthers, just after dehiscence, are so placed in relation to the entrance that butterflies must necessarily smear their heads and probosces with pollen as they thrust the latter organ along the grooves. After that has happened, the filaments bend to one side or stoop down beneath the laminæ of the petals, and then other stamens come into play, their anthers being held, as the first were, in front of the grooves running down the petals. In the Ranunculaceæ—*Eranthis*, *Helleborus*, *Isopyrum*, *Nigella*, *Trollius* (see fig. 267 [11])—a large number of stamens surround the central multiple pistil in several whorls. They are themselves encompassed by a circle of very small trumpet-shaped or tubular petals filled with honey, the so-called nectaries, and these are in their turn surrounded by large floral leaves, white, yellow, red, or blue in colour, which descriptive Botanists have designated as petaloid sepals. Shortly

after the interior of the flower becomes accessible, owing to the opening of these sepals, the anthers belonging to the outermost whorl of stamens dehisce. Their filiform filaments have in the meantime undergone elongation, inflection, and torsion to the extent necessary to bring the anthers exactly over the opening admitting to the little cups full of honey. Insects cannot suck the honey without brushing against these anthers. The next day the stamens of the first whorl move in an outward direction towards the sepals, their place being at once taken by the stamens of the next whorl nearer the centre of the flower. By the third day these, too, are reflexed and replaced by the members of the third whorl; and the process continues until all the stamens in turn have set their anthers over the nectaries. The punctuality and exactitude with which the whole series of operations is carried out is most extraordinary.

The same phenomenon may be observed in the flowers of the Grass of Parnassus (*Parnassia palustris*). Only here the number of stamens is limited to five, and one anther at a time is set in the way of alighting insects as is shown in fig. 267 [4]. The honey is secreted in two small oblong depressions on the inner face of certain curious fimbriate leaf-structures which are inserted between petals and stamens (267 [5]). If an insect in search of honey alights from above on the middle of the flower, it is certain to brush its proboscis against the particular anther which has set free its pollen that very day, and is itself in close proximity to the approach to the honey. The Grass of Parnassus possesses in addition another extremely interesting contrivance correlated with the movements of those insects, which, instead of alighting from above, settle on the edges of the petals. When such an insect moves from the margin of the expanded petals towards the nectaries it encounters a barrier in the form of railings composed of the radiating arms of the nectariferous scales. This barrier is not, however, insurmountable; its radiating arms do not secrete any viscid substance or terminate in sharp points, but are surmounted by round yellow knobs, resembling pins' heads (see fig. 267 [5]). The insect easily climbs over this obstacle without hurting itself, and then finds itself on the side of the scale where the nectaries are. But in doing so, it is brought so nearly to the middle of the flower that it is sure to touch the anther, which, having opened that very day, occupies the position commanding the passage to the nectar. We have here an instance of the adaptation of a flower to different visitors. Both those which settle from above and those which crawl from the edges of the petals are obliged to brush against the effective anther in the middle of the flower and besmear themselves with its pollen.

In all these cases the pollen pours in copious quantities from the anthers and forms either puffy masses which cling to the gaping loculi, or else a viscid mantle clothing the slender style, when that organ has been used to sweep it out of a tube of syngenesious anthers. Insects, on visiting the flowers, come into immediate contact with the pollen, it being in no way covered or wrapped up, and being obtruded so directly in the path that to avoid it would be impossible. In the next series of plants there is a certain amount of difference in this respect. The pollen

is not accessible direct, but is concealed in tubes or recesses, and the covering must be removed before an insect can be besmeared. In the composite flowers of the genera *Onopordon* and *Centaurea*, to which belongs, amongst others, the well-known Corn-flower (*Centaurea Cyanus*), the anthers are borne on slender filaments, and, as in all Compositæ, are connate into a tube, in which is concealed the upper portion of the style. The dehiscence being introrse, the pollen is deposited on the style. In the majority of Compositæ, the style then grows in length and pushes the pollen up beyond the top of the tube. But this is not the case in *Onopordon* or *Centaurea*. No elongation of the style occurs, and the pollen remains concealed in the tube. If, however, an insect sets foot on the central part of the capitulum and comes into contact with the stamens as it clambers over the florets of the disc, the filaments immediately contract, drawing back the sheathing anther-tube and leaving the pollen exposed on the top of the style, which is then brushed against by the under surface of the insect. The same result is achieved by different means in certain Papilionaceæ. The well-known *Cytisus*, *Melilotus*, *Trifolium*, *Onobrychis* are instances of one group. The front pair of petals, which is known as the keel, and serves as an alighting-place for insects, forms a receptacle with a very narrow opening at the top. In this are concealed the ten stout, partially connate filaments, and the anthers borne by them. When a humble-bee settles on the keel and inserts its proboscis into that part of the flower where honey is to be found, the keel is pressed down by the insect's weight, and the anthers are in consequence exposed, whilst the pollen resting upon them is rubbed off on to the under surface of the insect. The moment the insect leaves the flower the keel springs back to its former position, and once more conceals the anthers which, as a rule, have only parted with a portion of their pollen. The same process is repeated on occasion of each fresh visit, and as many as four different insects may thus be dusted with pollen from the same flower. In *Lathyrus*, *Orobus*, *Pisum*, *Vicia*, the phenomenon is in the main the same, but these plants have a special brush developed in connection with the style which sweeps the pollen out of the keel, where it has been deposited by the anthers, at the same moment as the insect alights on the flower. The insect is thus certain to carry away pollen on the under parts of its body.

The transference of the pollen in the Hemp Nettle (*Galeopsis*) and Monkey-flower (*Mimulus*) to the bodies of insects is also attended by a curious phenomenon. A stamen of *Galeopsis* is shown in fig. 216 [19], p. 91. The corolla is bilabiate, and beneath the arch of the upper lip are two pairs of stamens, one pair behind and the other in front of the stigma, which is bilobed, and has the property of shutting together its two component flaps in response to contact. Each of the anthers of the pair behind the stigma is box-like, and divided by an internal septum into two compartments capped by lids. If a needle is inserted into the flower so as to touch the anthers, the lids spring open, disclosing the pollen, which sticks to the needle; a similar action occurs when an insect visits the flower.

These cases, where the pollen has first to be uncovered by the insect before it can be carried away, are not more remarkable than those wherein pollen-masses

are concealed in niches, and are caused to adhere to the bodies of intruding insects by means of a special organ, and are then drawn out of their hiding-places. This method of transferring the pollen is especially characteristic of Orchids, and is extremely interesting. It will be worth while to consider it in some detail in connection with a few well-known instances, and for that purpose it will be necessary to begin with a general description of the peculiar structure of the flower in Orchids. In all species of Orchidaceæ the ovary is inferior, and at the flowering season resembles a pedicel. It bears at the top two tripartite whorls of floral leaves, one standing just above the other. Two segments in each whorl are alike in form, whilst the third is different. The difference is most conspicuous in the case of the odd segment of the inner whorl, and it is called the lip or *labellum*. Often it really resembles a lip, but not uncommonly it assumes the shape of a sabot, boat, or basin, whilst, in other cases, it is like an outstretched tongue, or even the body of a spider or some insect, bee or fly (see fig. 257[2], p. 226). The labellum is frequently lobed, and may also be fringed or slit up into long curling strips. In fact it exhibits an endless variety of configuration, and to it is mainly due the extraordinary appearance characteristic of Orchids. The ovary itself is produced in most Orchids above the two perianth-whorls, and rises up in the middle of the flower as the so-called *column*. This structure, which bears the stamen and the stigmatic surface, is always opposite the labellum, so that the approach to the bottom of the flower lies between the two. There are *two* stamens in the few Orchids allied to the already-mentioned Lady's Slipper (*Cypripedium*; see figs. 267[1] and 267[2]), but throughout the others only *one* stamen in each flower develops pollen. The filament can only be identified by careful examination and dissection of the flower; externally it is not visible. Usually the anther or pair of anthers is imbedded in pits or recesses in the column, or is adnate to one face or to the top of the column. In the flowers of the Helleborine (*Epipactis latifolia*, fig. 268[2]), and many other Orchidaceæ, on either side of the one stamen, which has a fully-developed bilocular anther, may be seen an abortive stamen in the form of a triangular tooth. The column bears, in addition to the stamens, a stigmatic surface corresponding to the tips of the three carpels. In the group of Orchids represented by the Lady's Slipper (*Cypripedium*) all three are capable of taking up pollen; in all other Orchids only two stigmas are receptive, and they are usually merged together into a single disc or plate; the third stigma being transformed into the so-called *rostellum*, a structure which plays an important part in connection with the processes now to be described. The rostellum assumes the most various forms in different Orchids, and special relations subsist between it and the anther. In many cases the rostellum is a beak-like structure, situated betwixt the solitary stamen and the stigmatic surface; it marks, so to speak, the frontier between these two structures. Certain portions of the rostellum disintegrate, forming a tough and extremely sticky mass like bird-lime, which, in most cases, takes the form of a wart. The anther is bilocular. The loculi contain each a clavate pollen-mass or *pollinium*, and open betimes—often indeed, before flower is open. After dehiscence

the pollinia may be seen peeping out of the longitudinal slits in the loculi with their narrower extremities connected with the adhesive portion of the rostellum (as in fig. 268[2]). The manner in which this connection is established varies greatly, according to the species, and cannot be discussed here; all we need note is the fact that the union is so strong that the two pollinia are drawn out of their hiding-places and carried away by any object which, coming into contact with the rostellum, removes the viscid mass from it. The Broad-leaved Helleborine (*Epipactis latifolia*), a plant of wide distribution in Europe, exhibits extremely well all the peculiarities of Orchids above referred to (see figs. 268[2] and 268[3]). The upper part of the labellum is excavated, and contains a copious supply of honey. Above the labellum is the quadrangular stigma (fig. 268[2]) borne by the column, and surmounting this is the wart-like and projecting rostellum (a white dot in the figure), whilst the anther crowns the column. The two pollen-masses developed in the anther are connected with the viscid portion of the rostellum. Fig. 268[4] shows what the pollinia look like when they are drawn out of the anther. The honey secreted in the cavity of the labellum is easily accessible to insects with short probosces, and the flowers of Helleborine are therefore much frequented by wasps. I have selected *Vespa Austriaca* for illustration, as I have often observed wasps of that species on the flowers. On alighting the insect holds on with its legs to the embossed parts of the lip and proceeds to lick up the honey filling the cavity, beginning at the bottom and working up to the top. During the latter part of the operation its forehead must inevitably come into contact with the viscid projecting rostellum, which at once adheres to it (see fig. 268[5]). In withdrawing from the flower, when the feast is over, the wasp draws the two pollen-masses attached to the viscid rostellum out of the anther-loculi, and flies away into the open air adorned with this curious head-dress (fig. 268[6]). Not satisfied with the meal afforded by a single flower, it straightway seeks another and behaves here in the same manner as it did on the first occasion. During the time of flight from one flower to another the pollinia, sticking to the wasp's forehead, undergo a gradual tilting forward, the sticky gland remaining fixed at the same spot, but the pollinia becoming depressed; as a consequence of this change in their position, the pollinia are not shoved into the anther of the next flower the wasp visits, but are pressed against the quadrangular stigma (see fig. 268[7]). This depression of the pollinia is much better marked in many other common Orchids, however.

In all essential respects the process above described is common to the majority of Orchids where the labellum has a downward inclination and there is only a single anther; but great variety prevails in respect of accessory details, as indeed is to be expected, when we consider the wide divergencies existing in the forms of the flowers and of their insect-visitors. A brief reference to two of the most striking modifications is all we can give here. The greatest variation is exhibited, as we said before, by the labellum and the rostellum. In some genera—in the Twayblade (*Listera*), for example—the part of the lip which contains the honey is not bowl-shaped, but in the form of a long, narrow furrow, and the secretion

is licked up by small beetles. In other instances the back of the lip is produced into a spur lined with cells full of sweet juice, to which insects obtain access by piercing the walls of the cells. The genus *Orchis* affords an example of this. Honey of a sort peculiarly attractive to butterflies is secreted in the tubular spur in other cases, such as *Gymnadenia* and *Habenaria* (see fig. 258 [9], p. 227).

Two separate particles of viscid matter are often produced on the rostellum, each being in connection with one only of the pollen-masses (e.g. *Habenaria*

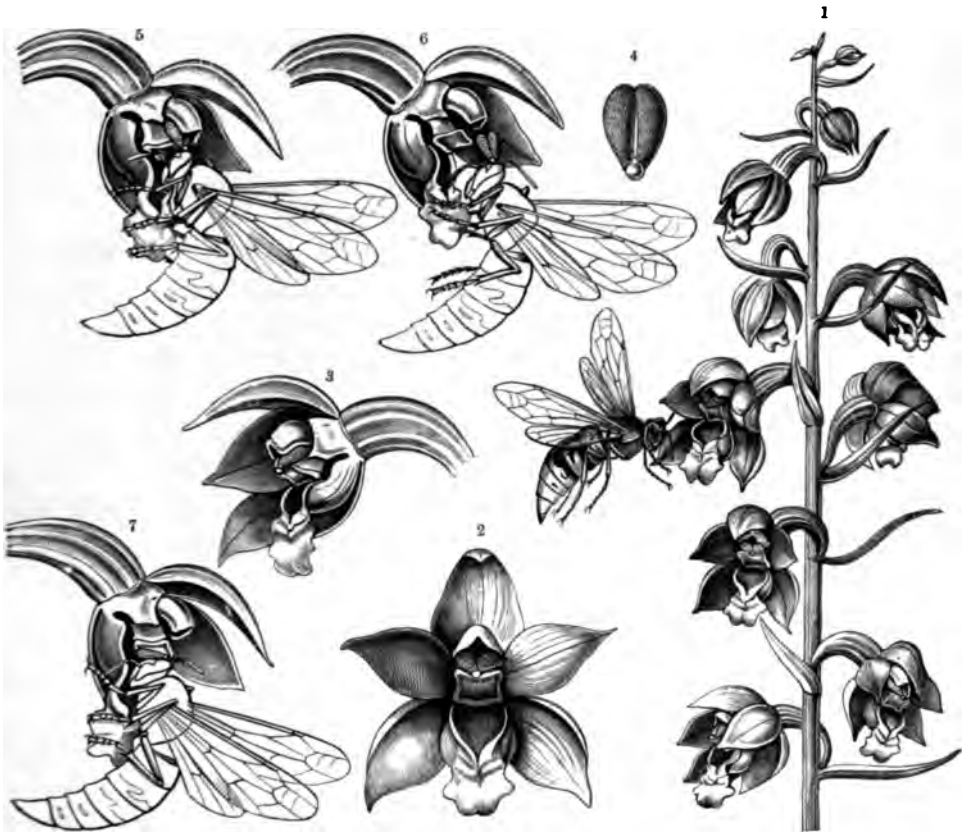

Fig. 268.—Withdrawal and deposition of pollinia in the flowers of an Orchid

Flowering spike of the Broad-leaved Helleborine (*Epipactis latifolia*) upon which a wasp (*Vespa Austriaca*) is alighting. [2] A flower of the same seen from the front. [3] Side view of the same flower with the half of the perianth towards the observer cut away. [4] The two pollinia joined by the sticky rostellum. [5] The same flower being visited by a wasp, which is licking honey and at the same time detaching with its forehead the tip of the rostellum together with the pair of pollinia. [6] The wasp leaving the flower with the pollinia cemented to its head; the pollinia are erect. [7] The wasp visiting another flower and pressing its forehead with the pollinia (which in the meantime have bent down) against the stigma. [1] nat. size; the other figures × 2.

chlorantha, the Large Butterfly Orchis). Insects then frequently only draw one of the pollen-masses out of the anther, instead of both, as they leave the flower. In species of the Twayblade genus (*Listera*) the rostellum is scale-like and arches over the stigmatic surface. At the commencement of the flowering period it is not connected with the pollinia, but the moment it is touched it exudes a drop of viscid fluid which sticks, on the one hand, to the body touching

it, and, on the other, to the pollinia surmounting the rostellum, and, hardening almost instantaneously, cements them together. The flowers are visited by small Hymenoptera belonging to the genera *Cryptus*, *Ichneumon*, and *Tryphon*, and still more frequently by little beetles of the genus *Grammoptera*. When an insect of any one of these genera lands on the labellum and proceeds to lick the honey-secreting furrow from the bottom to the top, it finds itself, towards the conclusion of its meal, in contact with the projecting edge of the rostellum. In a moment the pollen-masses are cemented to the forehead of the insect in the manner described, and are subsequently carried away upon a visit to another flower.

Strange to relate, the viscid masses sometimes adhere to the eyes of insects, although there can be no doubt that their power of vision is thereby curtailed. This occurs, in particular, in those Orchids where the anther-loculi and pollinia diverge from one another towards their bases and are connected with two separate viscid masses pertaining to the rostellum. In the flowers of *Habenaria montana* the pollinia are inclined to one another at an angle of 70° and form a kind of yoke under which it is necessary for butterflies to insert their heads if they want to suck the honey from the long spur. Thus the viscid discs, and, through their intervention, the pollinia are certain to attach themselves to either side of the intruder's head, and the eyes are frequently the spots where the adhesion happens to be effected. The genus *Habenaria* is also of interest inasmuch as it illustrates the fact that the particular minor variations in floral structure which are used to differentiate species always possess some special significance in relation to the visits of insects. The *Habenaria Hookeri* of the New World differs from the *Habenaria montana* of the Old World in having in the middle of the stigma a projecting lobe, the presence of which results in the formation of two entrances to the spur containing the honey. A butterfly visiting the flower only inserts its proboscis into one of the two passages, and therefore comes into contact with only one of the viscid discs and carries away but a single pollinium. Yet another arrangement is found in *Habenaria bifolia*, the Lesser Butterfly Orchis, which is widely distributed in Europe and Asia. In this species the pollinia lie nearly parallel and above the entrance, and they usually adhere simultaneously to one eye of the Sphingidæ which visit them (see fig. 258 [11], p. 227), or to the base of the proboscis in the case of nocturnal Lepidoptera (Noctuæ of the genera *Agrotis*, *Hadena*, and *Plusia*). In the various species of *Gymnadenia* the pollinia adhere to the sides of the probosces of the small Noctuæ which suck their honey, whilst in the Musk Orchis (*Herminium Monorchis*) they become attached to the front feet of such little Hymenoptera and beetles as come to lick their sweet store. A long series of contrivances showing a wonderful correlation between the forms of flowers and those of flower-seeking insects might be added to these examples.

At the time when insects visit the flowers, the Orchids hitherto referred to, all of which have erect inflorescences, have their labella turned towards the

ground owing to the stalk-like inferior ovaries being twisted through 180°. Only quite a few Orchids, on the other hand, retain the parts of the flower in the same positions, after the bud is open and ready for insects, as were occupied by them in the bud. *Epipogium aphyllum*, a remarkable plant, which has been already referred to in respect of its peculiar mode of life (see vol. i. p. 111), may be taken as a type of this group. As shown in fig. 257 [10], p. 226 of the present volume, five of the perianth-segments of *Epipogium aphyllum* are long and narrow and slightly incurved. These segments inclose a space in the same sense as the curved fingers of a hollow hand may be said to do so, and in the middle of the space the column presents itself in the shape of a slightly ascending platform for insects to alight on. Arching over it is the sixth leaf of the perianth, the labellum, which resembles a cowl or helmet and causes the whole flower to look somewhat like that of Monkshood. Honey is concealed in the interior of the cowl, and in order to reach it the humble-bees which frequent this Orchid are obliged to crawl up the landing-stage with their bodies in contact with it, that is to say, with the column bearing the stigma and anther. The separate parts of the flower here are in the reversed position as compared with ordinary Orchids, where the labellum is the lowest member. The column bears the anther at its lower extremity, then comes the rostellum, which develops an extremely sticky disc, and still higher up, the steeply-sloping wall of the stigma (see fig. 257 [12]). The oval pollinia are attached to the viscid disc of the rostellum by long ductile filaments or pedicels (see fig. 257 [13]), and are covered over by a membranous hood, the anther-case. When an individual of the species of humble-bee named *Bombus lucorum*, a frequenter of shady woods, alights on the column of a flower of *Epipogium aphyllum* and proceeds to crawl from the lower edge of that structure towards the honey concealed in the galeate labellum, it does not at once come into direct contact with the pollinia, they being covered by the hood-like anther-case, but the viscid disc of the rostellum immediately adheres to the under part of the insect's body. Afterwards, when the bee leaves the flower, the anther-cap is thrown back and the two pollen-masses attached to the viscid disc are drawn out of their niches and carried away (fig. 257 [13]). The manner of their transference to other flowers will be discussed in the next chapter.

In many respects similar to these Orchid-mechanisms for promoting a transfer of the pollen are those prevailing in the flowers of Asclepiadaceæ, where the pollen masses are fastened by special organs of attachment to the feet of insects. Here again the pollen is in the form of pollinia connected together in pairs, and one cannot look at them without being reminded of the analogous structure in Orchids (see fig. 269 [4]). On nearer inspection, however, important differences are discovered to exist. In the first place, the little knob ("corpusculum") connecting the two pollinia is not soft and viscid as in Orchids, but is a hard, dry implement with two arms capable of holding any small delicate object by gripping it like a clip; secondly, the pollinia are not clavate or of pasty consistency, but are in the form of

shining horny leaflets; and thirdly, the two pollinia which are attached to the clip-like body by ligulate strands belong to two adjacent stamens instead of to a single one. A transverse section through the flower of *Asclepias Cornuti* (see fig. 269[3]) shows in the centre a five-sided column; adnate to each of its sides is a tumid bilocular anther with membranous wings running down its lateral margins. The wings are not appressed to the column, but are reflexed, and stand out in pairs, with the free margins of the two wings in each pair converging towards one another. This produces the same effect as if the anthers coating the central column were slit through longitudinally in front of every corner of the pentagon. Owing to the fact that the swollen part of each anther bears a curious excavated structure, it comes about that the pollen-producing portions of the anthers are nowhere visible externally save the membranous wings or the five apparent slits, as is shown in

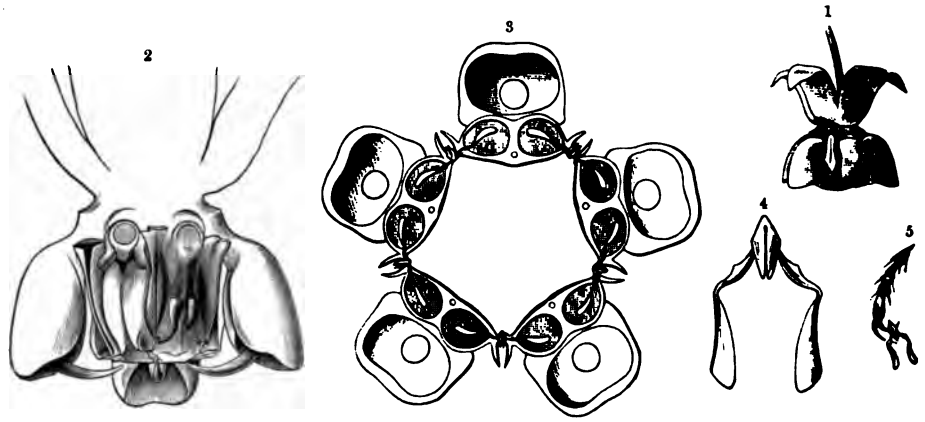

Fig. 269.—Clip-mechanism for fastening the pollinia of *Asclepias Cornuti* to the feet of insects.

[1] Flower of *Asclepias Cornuti* seen from the side. [2] The same magnified and with two staminal appendages and the front wall of an anther cut away. [3] Transverse section through the same flower. [4] Corpusculum (the clip) with two pollinia. [5] Foot of an insect with pollinia fastened to it by the clip. [1] nat. size; the other figures × 2-5.

figs. 269[1] and 269[2]). The hollow staminal appendages are full of honey, and each is embellished by a central process shaped like a horn. At the back of every one of the five slits is a little clip-like organ from which proceed ligulate strands connecting it with the pollinia in the adjacent loculi of two different anthers (loculi have vertical shading in fig. 269[3]), the pollen-mass in the left loculus of the anther to the right of the slit being thus associated with the pollen-mass in the right loculus of the anther to the left of the slit. The abundant honey in the staminal appendages emits a scent perceptible from afar, and attracts numberless insects to the flowers. The honey, being stored in a very superficial position, is accessible to insects with short probosces, and, therefore, the chief visitors besides hive- and humble-bees are wasps and Fossores, and these bright-coloured glossy insects—especially the splendid Scolias (*Scolia hæmorrhoidalis, S. quadripunctata, S. bicincta*)—are a beautiful sight as they hover about the blossoms. During the time when the honey is most abundant the flowers are either nodding or pendent, and they offer no convenient place for the insects to alight upon, or from which

they can comfortably suck the honey. All parts of the flower are smooth and slippery, and the only way in which an insect can support its weight is by inserting its claws in the slits between the anthers. In endeavouring to take firm hold, the insect draws its claw from one end of the slit to the other, and so becomes attached to the clip-like organ at the back. When the insect's foot is withdrawn the two pollinia adherent to the clip are dragged out of their niches. One of the claws on that foot is then seen to be wedged between the arms of the clip, whilst the two pollinia are suspended from it (see fig. 269 [5]).

The subsequent history of the pollinia does not strictly belong to the subject of this chapter, but it will be convenient to follow them to their destination. The pollen-masses must be conveyed to stigmas of other flowers. The question is, where are these stigmas to be found? The pentagonal central column, surrounded by the five anthers, contains the ovary in its interior. The approaches to this organ lie through the so-called stigmatic chambers, which are situated close beneath the truncate end of the column, and open outwards. The chambers are concealed in the slits, just as were the clip-like organs, and insects occasionally come across them as they move their claws about in the recesses. If the foot inserted by an insect has pollinia already attached to it, they are thus introduced into the slit in a new flower, and as the insect feels about for firm support it thrusts the pollinia into the stigmatic chamber. When the foot is subsequently withdrawn, the ligatures attaching the pollinia to the little clip are broken, and the pollinia are left in the chamber, whilst the actual clip maintains its grip of the claw. A second organ of the kind with its pollinia may become attached to the insect's foot on this occasion, and the process may indeed be repeated a number of times. Insects caught after visiting flowers of *Asclepias Cornuti* have often been found to have from five to eight of these clips fastened to a single foot.

Other members of the Asclepiadaceæ have essentially the same mechanism, though differences in detail of course occur. Very interesting is the result of cultivating the asclepiad *Araujia albens* (*Physianthus albens* of gardeners) in regions in which it is not indigenous. This plant is a climber from S. Brazil and Buenos Ayres, and being an ornamental plant is cultivated in gardens in various parts of the world. In its own country it is visited normally by humble-bees, and the curious phenomenon to be described has not been reported as occurring there. But in other localities its sweet-smelling, tubular flowers are visited by hosts of moths, which are apparently unacquainted with the mechanism of the pollen-masses, &c., and get trapped by their probosces in the slit-like notches, which are present between the anther-wings. These wings are rigid, and the slit narrows upwards, and moths visiting the flowers for honey get their probosces jammed in the slits. The result of their struggles to free themselves is only to fix their probosces the tighter in the narrow end of the slit, and the moths die a lingering death with their heads concealed in the tubes of the corollas, and their abdomens projecting. Reliable testimony of this moth-catching propensity of *Araujia albens* is forthcoming from Massachusetts (Providence), from Italy (Cagliari), and from

the Orange River Colony. The victims include *Plusia precationis*, *P. Gamma*, and *P. chrysitis*, *Picris Brassicæ*, *Deilaphila Euphorbiæ*, &c.

This clamping of pollinia to the feet of insects is quite unique amongst phenomena of the kind observed in the whole realm of plants, and it would be scarcely surprising if people who have not seen the operation with their own eyes were to look upon it as the offspring of a botanist's imagination. There are, however, in the same category, four other cases of behaviour equally calculated to excite astonishment in the observer, and these are all the more remarkable from the fact that in them the transference of pollen to the bodies of insects is effected by means of special movements of different parts of the flower. The insects do not dust off the pollen by coming into immediate contact with it, but their entrance into a flower causes certain changes in the position of the various parts resulting in the pollen being sprinkled, thrown, or rubbed upon particular parts of the intruder's body.

I do not like comparing these contrivances in plants to the devices of human ingenuity; but the analogy existing between the various kinds of mechanism which effect the transfer of pollen and machines, invented by man, is so close that it would be affectation to refuse to take advantage of the fact that the action of these contrivances in plants can be rendered much more easily intelligible by describing them in terms which plainly indicate their resemblance to simple appliances in use in every household. We shall, therefore, differentiate the various kinds of mechanism for loading insects with pollen, which still remain to be discussed, into those provided with piston-apparatus; hammers, or percussive apparatus; springs, or explosive apparatus; and sprinklers.

To begin with, let us take the *piston-apparatus* in Papilionaceæ. In very many though not all Papilionaceæ the two lateral petals, called *alæ* or wings, converge towards their upper margins, along which they are in contact, so that they form a convex saddle arching over the keel. This arrangement may be seen, for instance, in *Coronilla*, the Horse-shoe Vetch (*Hippocrepis*), the Lupine (*Lupinus*), the Rest-harrow (*Ononis*), *Anthyllis*, and in the Bird's-foot Trefoil (*Lotus corniculatus*; see figs. 270[1] and 270[2]), the last being the species here selected for illustration. The wings are connected with the keel in a peculiar manner. Near the base of each wing is a projecting fold which exactly fits into a socket in the corresponding half of the keel (see figs. 270[3] and 270[4]). Thus wings and keel are locked together, and every pressure upon the pair of alæ is transmitted to the keel. Consequently when a hive- or humble-bee sets itself astride on the saddle-ridge formed by the wings, not only is the latter pressed down, but also the keel; and this movement is accompanied, to the astonishment of the observer, by the extrusion of a pasty vermicular mass of pollen through a small opening at the conical apex of the keel, and by the simultaneous adhesion of the pollen to the insect's belly, or sometimes to its legs. The process of expulsion is shown in figs. 270[5,6,7], where a number of stamens lying close together are seen to be thickened into clubs at the part just below the anthers. This bundle of stamens

shuts off at the free end of the keel a hollow cone which is open at the apex only, and the action of the stamens within the cavity is just the same as that of the piston inside a pump. When the keel is depressed by a force acting in the direction of the arrow (fig. 270[6]), the stamens, being fixed, are forced further into the conical cavity and push part of the pollen stored in it through the small orifice at the top. When the pressure ceases the keel returns to its former position. It has been ascertained by careful observations that the process of pumping pollen from a particular flower may be repeated eight times, provided that the keel is not pressed down too low, and that when the keel is depressed beyond a certain

Fig. 270.—Apparatus for pumping pollen on to the bodies of insects.

[1] *Lotus corniculatus*. [2] Single flower of the same × 2. [3] The same flower with the standard removed. [4] The same flower with the standard and the wings removed so as to expose the keel. [5] One component leaf of the keel removed; in the interior of the keel are seen the stamens, the longer ones clavately thickened towards their free extremities; the conical cavity above the anthers (which are empty) is full of pollen, and the style and stigma are embedded in the mass of pollen. [6] Depression of the keel in the direction indicated by the arrow, in consequence of which pollen is pumped out of the orifice of the conical cavity by the bundle of clavate filaments. [7] The keel still further depressed in the direction of the arrow so that the stigma is extruded through the orifice at the apex of the hollow cone.

extent the end of the style also protrudes through the opening (see fig. 270[7]) and comes into contact with the abdomen of the bee which is visiting the flower at the time.

This kind of pump-apparatus appears to be confined to papilionaceous flowers. On the other hand, the mechanism to be described next, which does its work by means of impact, occurs in flowers belonging to the most diverse families. In every case of the kind the movement of the filaments, which results in the transfer of pollen to the body of an insect, resembles the striking of the hammer on a bell, although the cause of the movement is not the same in the different flowers. Sometimes a two-armed lever is set in motion; sometimes there is a sudden recoil of the stamens due to their liberation, as it were, from a vice, and in a third class

of cases the filaments are irritable and on the slightest touch undergo a change of position analogous to the closing up of the leaves of the Sensitive Plant (*Mimosa*; see vol. i. p. 537) when subjected to a like stimulus.

The best known examples of the hammer form of mechanism occur in the genus *Salvia*. In no species of that large genus is it developed to greater perfection than in *Salvia glutinosa*, which we therefore select for illustration. The flowers of this Labiate are set laterally on the stem, and the under-lip serves as landing-stage for the humble-bees to alight on (see fig. 271). If a bee, after alighting, is to obtain the honey which is hidden in the back part of the flower near

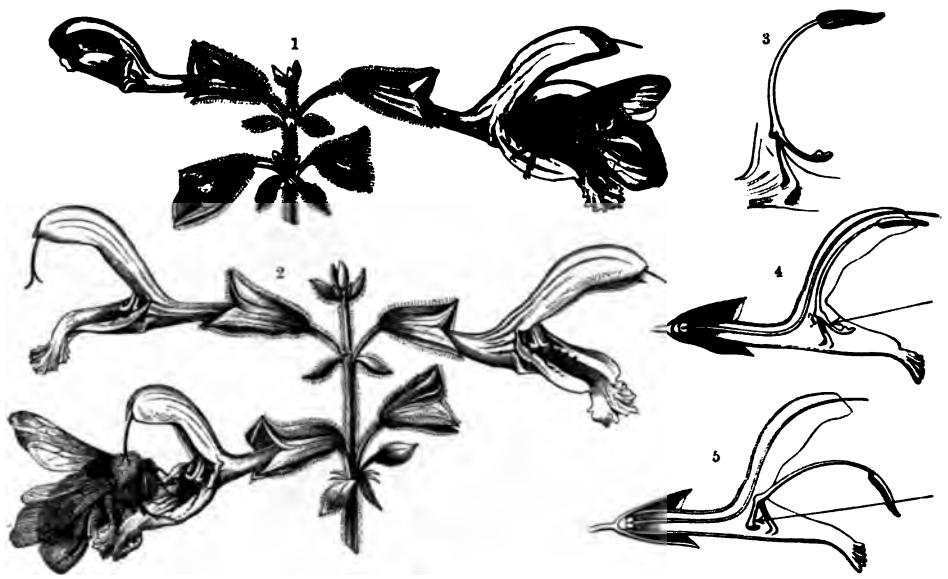

Fig. 271.—Transference of pollen to the bodies of insects by means of mechanism of the percussive type.

[1] Part of an inflorescence of *Salvia glutinosa*; the right-hand flower is being visited by a humble-bee, and the pollen-covered anther is in the act of striking the insect's back. [2] Another part of the same inflorescence with three open flowers in different stages of development: the lower flower on the left-hand side is being visited by a humble-bee which carries on its back pollen from a younger flower and is rubbing it off on to the deflexed stigma. [3] A stamen of *Salvia glutinosa* with rocking connective. [4] Longitudinal section through a flower of the same plant. The arrow indicates the direction in which humble-bees advance towards the interior of the flower. [5] Same section; the lower arm of the connective-lever is pushed backward, and in consequence the pollen-covered anther at the end of the other arm of the lever is deflexed.

the ovary, it must advance from the under-lip into the gaping jaws of the flower. It is there that the curious mechanism is set ready. On either side of the entrance is a stamen (see fig. 271 [3]) composed of a short, erect, firm, and immovable filament, and an anther borne at the extremity of a much elongated and slightly curved connective which rocks at the top of the filament. The connective is articulated to the filament in such a manner as only to be able to swing in the direction indicated in figs. 271 [4] and 271 [5]. The part of the stamen which is liable to be set rocking is a curved lever consisting of two arms of unequal length. The upper arm is the longer and terminates in the anther, whilst the under and shorter arm is somewhat thickened and spatulate at its free extremity. When a humble-bee pushes the lower arm in the direction of the arrow (fig. 271 [4]) the upper arm drops (fig. 271 [5]).

As the two stamens are close together and the lower arms of the connective practically touch one another, the upper arms fall simultaneously, and anyone observing the phenomenon from the side might think there were only a single rocking anther in the flower. Thus, when a humble-bee, making its way from the landing-stage of the under-lip to the floral receptacle, comes against the pair of short lever-arms barring the entrance, the anthers drop simultaneously upon its back and cover it with pollen (271 [1]). We shall show in a subsequent section that bees laden in this manner rub the pollen off on to the deflexed stigmas of the flowers they subsequently visit (271 [2]). The hammer-apparatus in the flowers of *Salvia officinalis*, which grows broadcast on the shores of the Mediterranean, only differs from the above in that a little pollen is developed in addition at the end of the lower arm of the lever, and is brushed off on to the head of the insect. The rocking part of the stamen in every species of *Salvia* must be looked upon as an anther with a specially modified connective. The connective is transformed into a long curved lever bearing an anther-lobe at each end. In *Salvia glutinosa* only the lobe at the upper end is polliniferous, whilst at the lower extremity there is a complete absence of pollen. In *Salvia officinalis*, on the other hand, a little pollen develops, as we have seen, in the smaller lobe at the end of the shorter arm also. In the numerous species of which *Salvia pratensis* is a type the filaments are extremely short, and the lower arm of the lever in each case is metamorphosed into a quadrangular flap or valve. The flaps of the two opposite stamens are joined so intimately together that they close the mouth of the flower like a trap-door. Each valve, however, has a little notch in the side adjoining the other, and the two notches coincide so as to form an orifice in the middle of the trap-door. Insects insert their probosces through this hole, and in so doing push the trap-door backwards and upwards. The valves of the trap-door being also the short arms of the lever-apparatus, their ascent is accompanied by the descent of the long arms, each of which bears an anther-lobe full of pollen at its extremity, and in this manner the upper surface of the insect's body is covered with pollen as it sucks the honey.

In the Lopezias indigenous to Mexico, the effect of the striking of insects by the anthers is to load, not the upper, but the under surfaces of their bodies with pollen. These plants (*Lopezia coronata, L. miniata, L. racemosa*) are remarkable for having only a single anther-bearing stamen in each flower. The stamen is wedged in a sterile, petal-like staminode inserted immediately below it; this staminode has its free end fashioned into the shape of a spoon. This spoon-shaped extremity affords the most convenient alighting-place, and the moment an insect settles upon it the staminode suddenly flaps down, whilst at the same instant the stamen concealed within it (being previously in a state of tension) springs up, striking the under surface of the insect's body and covering it with pollen.

The flowers of the Barberry (*Berberis*) have irritable filaments which cause the anthers to strike against insects. There are six stamens arranged in two whorls in each flower; they slope obliquely outwards, and are concealed in the concave

petals which are inserted behind them. Honey is produced in abundance from saffron-coloured swellings on the petals, and is to be found in the interior of the flower sticking to those sides of the filaments which face the ovary. Both hive-bees and humble-bees covet this honey and fasten on to the pendent racemes to obtain it. Often, in the very act of laying hold of a flower, an insect inserts its forelegs into it and touches the stamens; but even if this does not happen, the bases of the stamens are sure to be touched when the insect introduces its proboscis to suck the honey. The slightest touch administered to the lower third of a stamen's length acts as a stimulus, and results in an alteration in the tension of the tissues, and in a sudden backward movement or up-springing of the stamen. The anther is thus caused to strike upwards against the insect, covering its head with pollen, whilst the proboscis and forelegs are also besmeared, though to a less degree.

The transference of pollen to the bodies of insects takes place in the *Opuntia* in the same manner as in the Barberry. The comparatively large flowers of *Opuntia nana*, which grows in Dalmatia and near Sion in the Rhone Valley, &c., open at nine o'clock in the morning when the sky is clear. The fleshy four-lobed stigma may then be seen crowning the thick conical style and forming obviously the most convenient place for insects to alight on. The style rises out of a pit which contains a copious supply of honey, and is surrounded by a large number of erect stamens of different lengths. The dehiscent anthers are charged with pollen of a crumbly consistency; the filaments have the lowest quarter of their length coloured pale yellow and the upper part bright gold. If the golden region of the filament is touched, it curves inwards, forming a semicircular and slightly twisted bow, surmounting the honey-receptacle out of which the style rises. When a bee visits the flower, it settles first on the large stigma, which projects above the anthers, and then tries to clamber down to the honey. During this process contact with the irritable portion of the filaments is inevitable, and the moment it occurs the stamens that are touched bend over the bee and load it with their pollen which is easily detached from the anthers. It is amusing to watch this phenomenon and observe how quickly one after another the filaments bend over the insect, and administer their blows as it crawls down. The bee is not much alarmed by the inflection of the filaments, or by the taps it receives, but suffers itself to be loaded with pollen without making any fuss. It is able to brush it off subsequently and collect it in the "honey-baskets" borne on the tibiæ of its hind-legs. As the inflection of the stamens lasts at least until the insect leaves the flower, a further supply of pollen is sure to be rubbed off when the bee begins to retreat. Usually, when bees leave *Opuntia* flowers, they are dusted all over with the yellow pollen.

Part of the pollen, in the case where the anthers belong to a mechanism of the percussive type, is appressed and affixed to the insect's body, whilst part is brushed off owing to the movements of the creature when it takes its departure from the flower. In this respect the apparatus differs from contrivances of the *explosive* variety, which are adapted to besprinkle or bespatter insects with pollen. The explosion is due to a sudden up-springing of some organ, which may be the style, the filaments

or, as in a few Orchids, the anthers and rostellum. The number of these contrivances is very large, and I must therefore confine myself to an account of the most curious forms, beginning with the case of *Crucianella stylosa*, which grows native in Northern Persia, and is represented in figs. 272 and 274[1]. This plant belongs to the Stellatæ group of Rubiaceæ. Its rose-coloured flowers are conglomerated in terminal heads (274[1]), and scent the air with honey to a considerable distance. If one side of the corolla be removed, the first peculiarities that strike the observer are that the long slender style is twisted into a spiral, and that the thick stigma

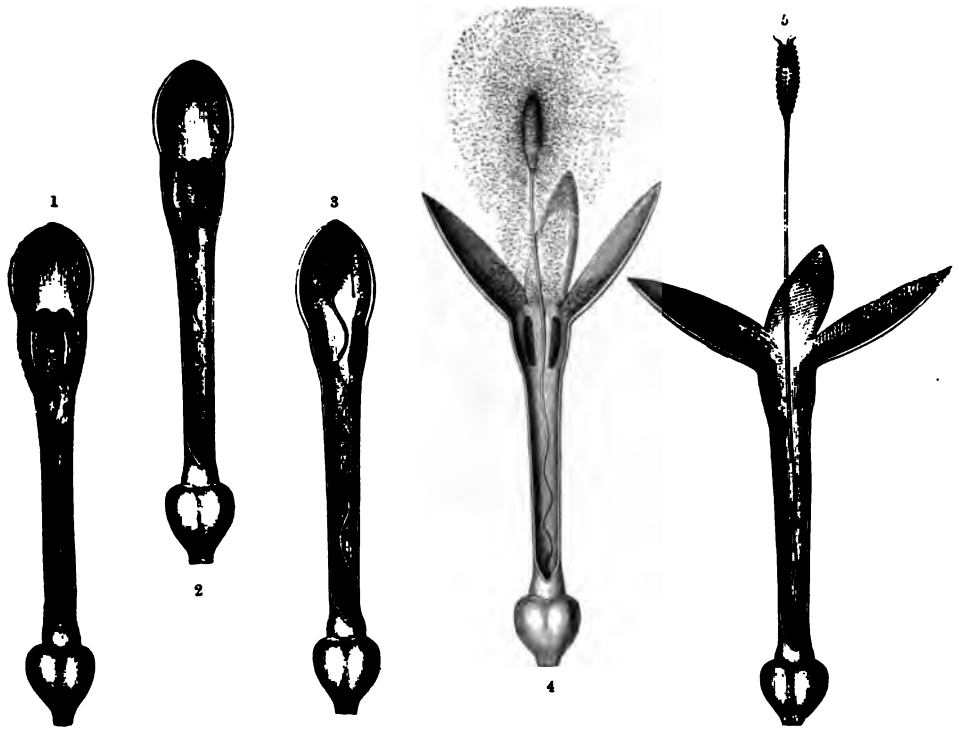

Fig. 272.—Explosive apparatus for the transfer of pollen to the bodies of insects

[1] Longitudinal section through the unopened flower of *Crucianella stylosa*; the papillose stigma wedged between the closed anthers. [2] The same after the dehiscence of the anthers; the pollen deposited on the papillose surface of the stigma. [3] The stigma covered with pollen has been carried up owing to the elongation of the style until it rests under the dome of the closed flower. [4] The corolla has burst open, and the style, springing up suddenly in consequence, is discharging the pollen from the surface of the stigma. [5] The style projects far beyond the corolla and bears the open two-lipped stigma which is now first mature and ready to be pollinated. All the figures × 4.

at the top of it is wedged between the anthers (see fig. 272[1]). The moment the anthers open the pollen pours out of the loculi and rests upon the papillose surface of the stigma (fig. 272[2]). Soon afterwards the style elongates and its coils relax somewhat, the result being that the stigma, with its coating of pollen, is carried up above the now empty anthers until it comes against the dome-shaped top of the closed corolla where its further ascent is stopped. At this stage of development (fig. 272[3]) the style is in a condition of such extreme tension that the instant the limb of the corolla opens it springs up, scattering a cloud of pollen from the surface of the stigma (fig. 272[4]). In the absence of insects this ejection of

pollen takes place spontaneously; but a sudden opening of the corolla-limb is caused if a small bee or fly chances to touch the top of a closed flower on its way to visit an open one, and the insect is then dusted with pollen from below as is shown in fig. 274[1]. The subsequent events occurring in these flowers will be described later on, and an explanation of fig. 272[5] will then be given.

The species of the genus *Schizanthus*, indigenous to Chili and Peru, one of which—*Schizanthus pinnatus*—is cultivated in our gardens as an ornamental plant, have long been known to possess mechanism for the explosive distribution of pollen. The most conspicuous object in the open flower of any of these plants is a single up-turned speckled lobe, whose function it is to attract insects. Beneath it are two smaller incised lobes which form a sort of keel. affording a convenient place

Fig. 273.—Explosive apparatus in a papilionaceous flower.

[1] Flower of *Spartium scoparium* (*Sarothamnus scoparius*) seen from the front, the keel closed. [2] Same flower with the keel open; the stamens previously concealed there together with the style have sprung up. [3] Side view of the same flower after the opening of the keel and springing up of the stamens. [4] One of the two component petals of the keel seen from within.

for insects to alight on. Fixed firmly in the furrow of this keel are two stamens, which are released the moment an insect settles on the keel and introduces its proboscis underneath the vexillary petal above described. The stamens then spring up, and the pollen is scattered out of the anthers.

The occurrence of a similar up-throwing of pollen in the flowers of the Yellow Corydalis and a few other species of the same genus (*Corydalis lutea, C. ochroleuca, C. acaulis*) has been already noted (p. 228) in the account given of the stirrup-shaped lobes on the sides of those flowers. We have only to add that the articulation of the projecting left-hand petal to the two contiguous median petals forming the saddle ceases the moment an insect sprawls upon the saddle and inserts its proboscis underneath the spurred petal. This disconnection has the immediate effect of causing the saddle to drop and the stamens hitherto concealed in the cavity to spring up. The meal-like pollen of *Corydalis* being liberated early, is by that time lying loose upon the anthers, and is ejected upon the under surface of the insect when the stamens are thus suddenly released (cf. figs. 257[3] and 257[4], p. 226).

The phenomenon of an upward discharge of pollen is also well exhibited in the Melastomaceæ and in many Papilionaceæ of the genera *Astragalus*, *Indigofera*, *Medicago*, and *Phaca*, as also in *Genista*, *Retama*, *Sarothamnus*, *Spartium*, and *Ulex*. We will select *Spartium scoparium*, a plant belonging to the Mediterranean Flora (figured in vol. i. p. 331), as a representative of this group. Figs. 273[1] and 273[2] show the front views of a flower of *Spartium scoparium*, and one

Fig. 274.—Transference of pollen to the bodies of insects by means of explosive apparatus.

[1] *Crucianella stylosa*; the pollen is being discharged from the flowers on to the belly of a hymenopterous insect. [2] *Spartium scoparium*; in the lowest flower the keel is still closed and stretched out horizontally; in the flower next above, the keel is depressed and the stamens have sprung up; the third flower is being visited by a Carpenter Bee (*Xylocopa violacea*), and is ejecting its pollen on to the under surface of the insect's body.

recognizes at once the large upturned standard, the two lateral petals and underneath them the keel composed of a pair of contiguous petals. Near the base of each keel-petal is observed a swelling and a depression (fig. 273[4]), which correspond with portions of the structure of the two wings, so that the latter pair of petals engages with the keel, and every pressure upon the wings from above affects the keel also. A blunt tooth may also be seen near the base of each of the wings (see fig. 273[3]). When the flower is closed the teeth are hidden under the standard; in the open flower they are pressed against the standard, and so keep the wings, and indirectly the keel, in a horizontal position.

In the keel are concealed a style and ten stamens, all in a state of tension like watch-springs. The anthers liberate their pollen very early, and it accumulates in the front part of the keel. When the pulvinate wings, and through them the keel, undergo pressure from above, the blunt teeth which fasten the wings and keel together slip down, and both wings and keel fall with a sudden jerk, whilst the stamens and style lying at the bottom of the keel spring up, throwing the mealy mass of pollen into the air. In nature the object to which the pressure on the wings is due is usually a largish insect, and the result is of course just the same, so that the under surface of the creature's abdomen receives the discharged pollen (fig. 274 [2]).

The pollen in these flowers being of floury or powdery consistency, a great cloud of dust is emitted whenever the explosive mechanism is brought into play. The same effect is produced as if the flowers exploded, and several of the plants in question—as, for instance, the various species of the genus *Schizanthus*—are called by gardeners "plants with explosive flowers". Apparatus for ejecting the whole of an anther's pollen at once in a single coherent mass are of much rarer occurrence. The flowers of a Brazilian shrub named *Posoqueria fragrans*, belonging to the order of Rubiaceæ, and those of a few tropical Orchids are especially remarkable in this respect. The blossom of *Posoqueria* reminds one in many ways of that of the Honeysuckle, exhibiting like the latter a corolla composed of a long horizontal tube and five short limb-segments which are somewhat reflexed when the flower opens. The opening takes place in the evening; the corolla is white, secretes honey at the bottom, and emits at dusk and during the night a pervading scent—all characteristics of a nature to indicate that the flowers are adapted to the visits of Sphingidæ. The abundant honey at the base of the tube can only be reached by the tongues of Sphingidæ; and only these insects, *e.g. Sphinx rustica*, whose proboscis is 15 mm. long, have been seen to visit the flower.

The five anthers are united into an oval knob directed obliquely downwards and containing the loosely-coherent pollen which escaped from the anthers before the expansion of the flower. The filament of the lowest stamen possesses a very considerable elastic tension acting upwards; those of the upper and lateral stamens have a similar tension outwards. The insect's proboscis has only one available point at which to enter the flower, and when in doing so it touches one of the upper stamens at a certain spot the tension of the stamens is released. The lowest stamen springs up with such violence that it hurls the loosely-coherent pollen against the insect's proboscis at an angle of 50° with the tube of the corolla, and with an initial velocity of about 3 mm. per second; at the same time it closes the entrance to the tube. The upper and lateral stamens spring at the same time to the sides, the empty anthers of an upper and a lateral stamen remaining coherent on either side. About twelve hours afterwards the lowest stamen extends itself again and leaves the entrance to the flower open once more. If a hawk-moth, after exploding a flower in the first stage, comes

to one in the stage under consideration, it is repaid for its startling reception in the former case by a rich supply of honey; and in thrusting its pollen-dusted proboscis down to the base of the flower it brings it in contact with the stigma, which stands in the middle of the tube.

The most noteworthy cases of Orchids furnished with expulsive mechanism

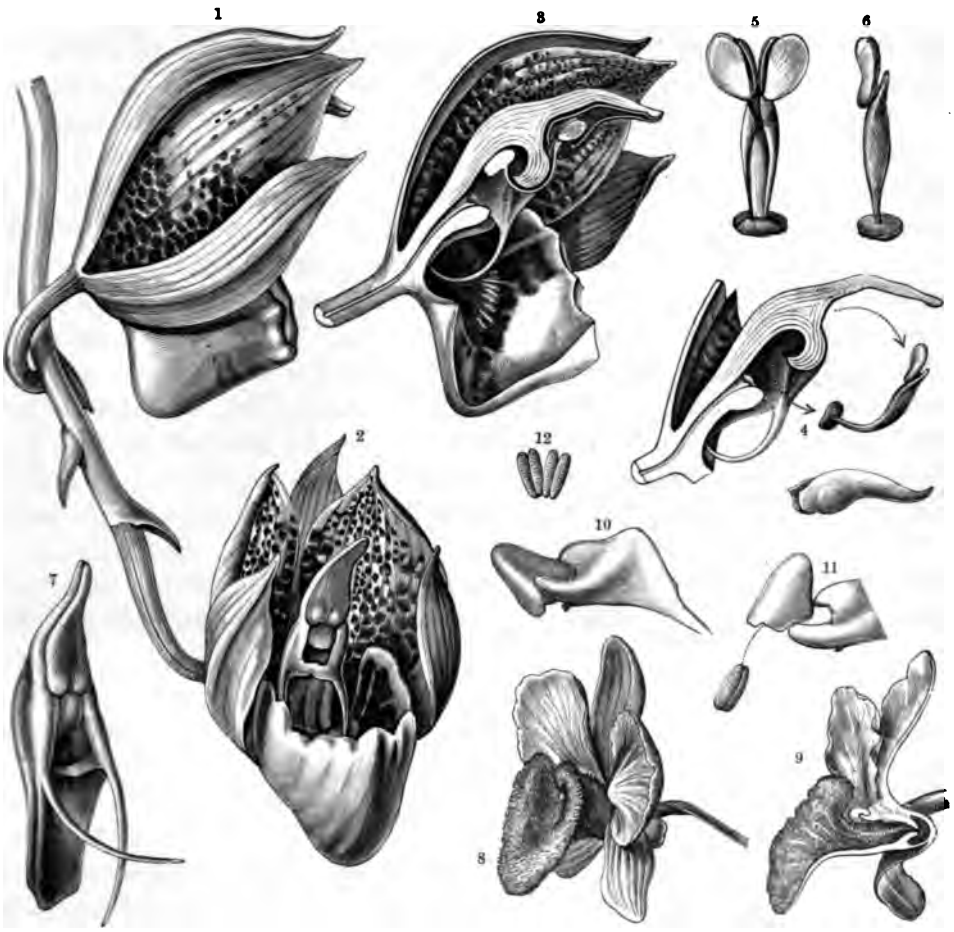

Fig. 275.—Expulsive apparatus in Orchid-flowers: flower of *Catasetum tridentatum*.

[1] Side view. [2] Front view. [3] Longitudinal section through the same; the band connecting the pollen-masses with the viscid disc is stretched like a bow over the protruding rostellum. [4] The pollen-masses and viscid disc are liberated and are being jerked away by the sudden straightening of the connecting-band; the anther-case which hitherto concealed the pollen-masses tumbles away at the same time (below). [5] Front view of pollen-masses, viscid disc, and the band connecting them; the margins of the band somewhat involute. [6] Side view of the same. [7] Column removed from the flower; towards the summit is the anther, below it the elastic connecting-band stretched like a bow; next the stigmatic chamber with its fleshy margins prolonged into two horn-like irritable processes. [8] Flower of *Dendrobium fimbriatum*. [9] The same in longitudinal section. [10] Side view of the hood-like anther at the end of the column. [11] The anther jerking back and ejecting the pollen-masses. [12] Pollen-masses of *Dendrobium fimbriatum*. [10], [11], [12] × 5; the rest natural size

are those of the genera *Catasetum* and *Dendrobium*. *Catasetum* will need a somewhat detailed account, for the reason that in this genus the process of expulsion ensues upon an external stimulus which does not act upon the mechanism in question direct, but is transmitted through a special organ. The column in the flower of *Catasetum* (see figs 275[1] and 275[2]), as in many other Orchids, rises

up over a hollow labellum. Near the apex of the column is the anther, and lower down the rostellum, whilst below the rostellum the column is deeply excavated. The edges of this pit are fleshy, and are prolonged into two curious processes resembling a pair of horns. These processes are curved and tapering, and are inclined obliquely forwards and downwards. In most species, including *Catasetum tridentatum* (here represented), the horns (or antennæ, as they are sometimes called) cross one another diagonally (see fig. 275[7]). Each horn, originally a ribbon-like lobe, is rolled up lengthwise so as to form a tapering tube. The substance of both horns passes without any definite line of demarcation into the tissue of the rostellum above. Although this tissue has been examined with the greatest care, nothing special has been found in it to account for the extraordinary irritability which it exhibits. It has been ascertained by experiment that any pressure on the lower extremity of the horn acts as a stimulus, and that this stimulus is at once transmitted upwards through the cells of the tissue to the part of the rostellum which forms the viscid disc. The slightest touch applied to the tip of one of the horns is instantly followed by the rupture of the tissue which has hitherto retained the viscid disc in position, and by the consequent liberation of that portion of the rostellum. The viscid disc had, however, in its turn served to keep a curved elastic band which attaches the disc to the pollinia on the stretch, and in its proper position (fig. 275[3]), so that when the disc is set free the band flies up and straightens itself up with a jerk. The viscid disc and the pollinia are torn from their recesses by the recoil of the band, and are carried with it in an ample curve away from the column, which till then has served as their common base (fig. 275[4]). During its flight the viscid disc goes first, and it naturally, by sticking to some object in the way, brings the pollen-masses to a standstill. From the time of its being shot off, the band connecting the disc and the pollinia is quite straight (see figs. 275[5] and 275[6]).

The expulsive apparatus exhibited by most species of *Dendrobium* is altogether different. In the species selected for illustration—viz. *Dendrobium fimbriatum* (figs. 275[8] and 275[9])—the column is capped by an anther in shape like a bell. The anther is septate, and contains in its loculi pollen-masses, which since they are unconnected with any viscid disc, are therefore liable to fall out of the anther in certain positions of the latter. The anther is borne by a slender subulate filament, to the extremity of which it is articulated in such a manner that a gentle push is sufficient to set it rocking. When the flower first opens, and before it has yet been exposed to any contact, the bell-shaped anther rests mouth downwards on a notch at the top of the column, and is held in that position by two tooth-like processes to the right and left of the notch (see fig. 275[10]). A push administered from the front displaces the anther and causes it to fly back, whilst the pollinia contained in it are simultaneously expelled (see fig. 275[11]). The pollinia being unfurnished with viscid discs (fig. 275[12]), it is not quite evident how the insects which supply the necessary stimulus on their visits to the flowers get loaded with the pollen. There is, however, every probability that the expulsion

is followed by a transference of the pollen to the bodies of the insects. Unfortunately we do not know of any observations having been made of the visits of insects to plants of this species in the wild state. Such observations might enable us to come to a sure conclusion on the subject, but so far all our results have been derived from flowers reared in hot-houses.

Next to the expulsive variety of mechanism comes the *sprinkling* variety. Pollen transferred by this kind of apparatus is always of mealy or powdery consistency, and is shaken out of the loculi where it is produced. Three modifications of this apparatus may be distinguished, viz.:—the sugar-tongs modification; that in which the anthers dehisce by terminal pores; and that in which the anthers are united into cones. In contrivances of the first kind, the filaments are like the arms of a pair of sugar-tongs, and the anthers borne by them are, when in the dehiscent condition, in the form of spoon-shaped receptacles or recesses, with the concave sides facing one another. Pollen of mealy consistency would not stay in open, upright spoons of the kind were it not for a special contrivance. In order to picture the state of things it is best to think of the action of a pair of sugar-tongs in which the end of each arm is fashioned into a spoon. When the tongs are closed the concave surfaces of the spoons are brought together, and form a receptacle in which sugar can be retained in the form of little solid bits, and even in the form of fine powder if the parts of the tongs fit well. The moment the two arms of the tongs are separated the contents held by the spoons drop down, and if in the condition of powder they must inevitably bepowder any object that may happen to be underneath. Now, this is just what occurs in connection with the sprinkling apparatus in the flowers of a large number of Acanthaceæ, Rhinanthaceæ, and Orobanchaceæ. Beneath the protective covering of the floral envelopes—most commonly under the upper lip of a bilabiate corolla—are found the stamens arranged two and two, with the anthers of each pair closed together like the two valves of a leguminous pod. They are kept in this position by the stiff staminal filaments, and the margins of the valves fit one another so exactly that not a single pollen-cell from the mass of floury pollen contained between them can fall out unless the structure is subjected to some particular shock. In some cases each pair of opposite valves is furnished with matted hairs which join the upper edges together. The form is then like that of a mussel-shell, and only the free margins can open. The moment the valves separate in the least, whether they are joined together at one part or not, the pollen spills out in accordance with the law of gravity. The direction of its fall is often determined by delicate hairs fringing the margin of the anther, the object being to prevent waste. The separation of the valves is caused by insects—and in tropical regions probably by humming-birds as well—when they press into the jaws of the flowers in search of the honey stored in the back-ground. In doing so the proboscis (or beak) is either pushed right between the valves, or it strikes against certain special processes with which the valves are furnished, or else the tense filaments bearing the valves are forced

asunder. The first is what occurs in *Bartsia alpina*. In the flowers of this plant the entrance is much narrowed, owing to the curving up of the limb of the under-lip, and close behind the entrance are found the anther-valves, which are comparatively large, and are edged at the top with matted hairs. Before an insect can reach the honey on the floral receptacle it has to force apart the lower edges of these valves, thus letting the pollen fall out upon itself. In the flowers of the Yellow-Rattle and Toothwort (*Rhinanthus, Lathræa*), the entrance is still more exactly defined, and the insect cannot deviate a hair's-breadth from it without sustaining injury. The filaments bearing the valves, which in this case are posted in the middle of the entrance, are beset with rigid prickles liable to injure an insect's delicate proboscis, and the only safe path to the receptacle lies between the ciliated anther-valves, which part asunder on being pushed with any moderate force (see figs. 277 [4, 5, 6]). In *Clandestina, Trixago*, and several other Rhinanthaceæ, the filaments are not furnished with prickles, but each anther bears a little downwardly-directed process which is pushed on one side by an insect entering the flower. The corresponding anthers are parted by the displacement of the processes, and the floury pollen is sprinkled upon the head and back of the intruder. In flowers of the Lousewort genus,—*Pedicularis asplenifolia, P. rostrata*, and many species allied to them—the anthers are hidden under the arch of the upper lip, and it is impossible for insects to come into direct contact with them. The path of the insects here lies somewhat deeper between the filaments, which they force apart, causing thereby a corresponding change in the position of all the different parts of the flower. In consequence the anthers also move asunder, and let fall the floury pollen hitherto wedged between them. A somewhat different mechanism is exhibited by several species of the genus *Pedicularis*, which may be represented by the common alpine *Pedicularis recutita* (fig. 276). The anthers in the flowers of this plant are borne on elastic filaments, and are regularly squeezed between the lateral walls of the helmet-shaped (*galeate*) upper lip. No separation of the valves is possible unless the galeate lip expands and becomes laterally inflated. This is brought about in a very curious manner. When a humble-bee alights it seizes the projecting upper lip and bends it down through an angle of about 30°, this action being facilitated by the presence of strong ribs at the base of the helmet on either side of the throat of the corolla which act like levers, and communicate their motion to the entire upper lip. In consequence of the inclination of the upper lip, the sides of the helmet, which up to this time are tightly stretched, bulge out laterally; secondly, the filaments bend in the same sense as the bulging sides of the helmet; and thirdly, the anthers themselves come apart pouring the

Fig. 276.—*Pedicularis recutita.*

[1] Entire flower. [2] Longitudinal section of the same. [3] Pollen falling out in consequence of the inclination of the helmet-shaped part of the corolla. × 3.

pollen-dust on to the insect's back. In order that this complicated machinery may do its work successfully, the insect must insert its proboscis at a certain definite spot through a little groove in the under lip, and for this reason all other spots where entrance into the flower might be attempted are barricaded. The margin of the upper lip, for instance, is thickly furnished with short-pointed prickles which the insects take care not to touch (*cf.* figs. 276 [1, 2, 3]).

The chief points of difference between the kinds of sprinkling apparatus hitherto described and that which occurs in Acanthus flowers (*Acanthus longifolius, A. mollis, A. spinosus*; see figs. 277 [1, 2, 3]) are that in the latter the anthers

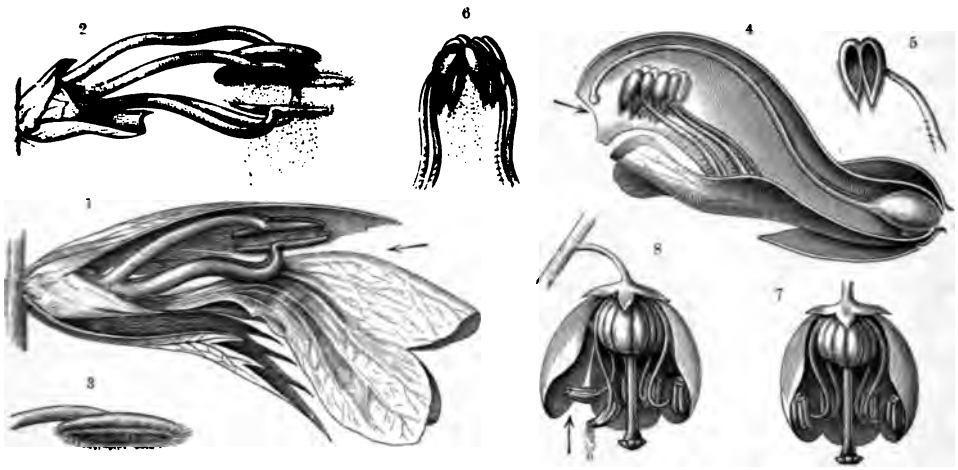

Fig. 277.—Sprinkling apparatus.

[1] Flower of *Acanthus longifolius* with some of the petals cut away. [2] Stamens of *Acanthus* illustrating the sugar-tongs principle; the anthers parted so as to let fall the pollen. [3] Single anther of *Acanthus* showing fringe. [4] Longitudinal section through the flower of *Rhinanthus angustifolius*. [5] Stamen from the same. [6] The four stamens of *Rhinanthus* seen from the entrance to flower; the anthers in contact at the top, parted below; the pollen falling out. [7] Flower of *Pyrola secunda* with some of the petals and stamens cut away. [8] The same; the anther is capsizing owing to the displacement of the petal which has hitherto kept it in position, and pollen is being sifted through the pores. The arrow in figs. [1], [4] and [8] indicates the direction in which an insect enters the flower. [1], [2] natural size; the rest × 2 to 5.

are unilocular instead of bilocular, and that the loculus resembles a long narrow niche rather than the valve of a mussel-shell. Each niche is edged with close short down, a provision which conduces materially to effective closure when the two anthers are in contact. The filaments look as if they were made of ivory; they are unusually strong, and are not so easily pushed asunder. Sturdy humble-bees of large size alone are able to displace these filaments, and the result of their doing so is to part the anthers and cause a shower of floury pollen to descend upon their bodies.

A form of sprinkling apparatus very different from the sugar-tongs variety, with its spoon-shaped anther lobes, is exhibited where the anthers act like pepper-castors. Contrivances of this type occur chiefly in bell-shaped blossoms which are either pendent or nodding. The anthers are furnished at or near their free extremity with two little pores, and are so placed inside the bells as to have the holes facing downwards at the moment when the pollen is to be scattered. The

pollen is of a floury consistency and is tightly compressed in the anthers, but it is sifted out intermittently, a little at a time, somewhat as powdered sugar is shaken through the holes of a castor. In some cases the anthers are suspended inside the bells with their pores downwards from the very commencement, as, for example, in the flowers of the Snowflake (*Leucojum vernum*) and those of the Cowberry (*Vaccinium Vitis-idœa*); but in others the elastic filaments are reflexed and hold the anthers at first with their pores upwards, facing the receptacle of the pendent flower. In order that the pollen may fall out of this class of anthers (with pores directed upwards), they must be turned upside down. This inversion is effected by insects, and as an example we will describe how it occurs in a Winter-green (*Pyrola secunda*). The filaments are curved into the shape of the letter S and are in a high state of tension, and the anthers borne by them are held in position, with their pores directed upwards, by the pressure of the petals (see fig. 277[7]). When an insect visits the bell it displaces the petals with the result that the filaments straighten out and the anthers are inverted (fig. 277[8]). In a large number of instances the anthers are furnished with special appendages against which insects are sure to strike when they enter the flower, whereupon a little pollen invariably pours out. The Snowdrop (*Galanthus*) has simple rigid points depending from the free extremities of the anthers and standing in the way of insects, and so also have *Cyclamen*, *Ramondia*, and many other plants belonging to widely-different families. The Strawberry-tree (*Arbutus*) and the Bearberry (*Arctostaphylos*; *cf.* fig. 263[1] p. 240) have two little horns projecting from the back of each anther, against which insects knock in their quest for honey, the result being that the whole anther is shaken and scatters pollen through its pores.

Anthers which dehisce by pores and act in the manner above described are usually associated with actinomorphic (*i.e.* radially symmetrical) and either pendent or nodding flowers, and all the cases we have examined hitherto have in fact been of pendent or nodding bells of perfectly regular conformation. Of the few zygomorphic flowers (*i.e.* symmetrical about one plane only) furnished with anthers of the kind I can only refer briefly to the Calceolariæ and Melastomaceæ. In these plants the anthers rest on short filaments, and are easily set rocking like those of *Salvia*. But whereas in the flowers of *Salvia* the anthers dehisce longitudinally and contain pollen of viscid consistency, those of the Calceolariæ and Melastomaceæ open by pores, whilst the pollen contained in them is of mealy or powdery consistency. The anthers are set swinging by insects knocking against them, and the pores being thus lowered the pollen comes tumbling out on to the bodies of the intruders.

The third form of sprinkling apparatus consists of a whorl of stiff stamens grouped together so as to form a hollow cone. The anther belonging to each stamen is composed of two lobes which open by longitudinal fissures and after dehiscence are simply open niches. The pollen is in the form of meal or powder, and in order to prevent it from falling out of the niches before the right time a special contrivance is necessary to keep them closed. This result is attained by

two different methods. According to one method the anther-lobes are pressed firmly against the style round which they stand in a small circle; according to the other the lobes of adjacent anthers face one another and are closed as tightly together as were the anthers of the sugar-tongs-like stamens already described. The first arrangement occurs in *Soldanella* (see figs. 278[1, 2, 3]), the latter in many species of *Erica* and of Boragineæ (see figs. 278[4, 5, 6, 7, 8, 9, 10]). In both cases the cone is composed of four or five lanceolate anthers, and the pollen is concealed in eight or ten long narrow loculi which part and let their contents fall if the cone is displaced to the slightest extent. If an insect touches the cone anywhere, as it must do to insert its proboscis, it dislocates the closely-fitting parts and causes a little shower

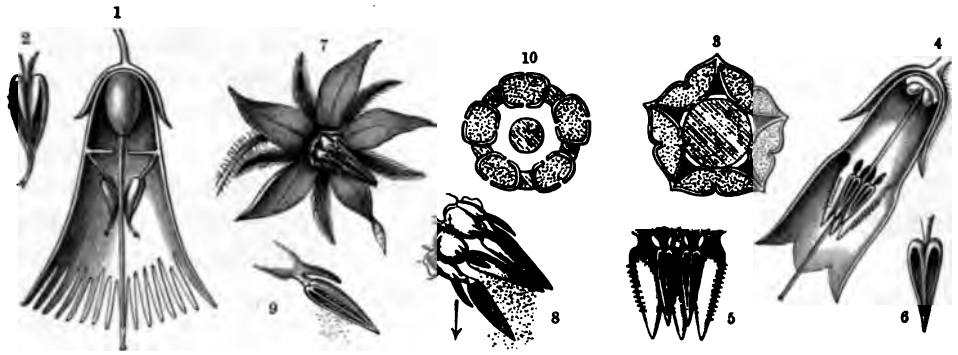

Fig. 278.—Sprinkling apparatus.

[4] Longitudinal section through a flower of *Soldanella alpina*. [2] Stamen from the same seen from that side which is in contact with the style. [3] Diagram of transverse section through the style and the five anthers adherent to it; the lightly shaded part is the style, the darker shaded portions are the connectives, the dotted portions are the pollen. [4] Longitudinal section through a flower of *Symphytum officinale*. [5] Two stamens and three scales of same beset with prickles. [6] Single stamen of *Symphytum*. [7] Flower of *Borago officinalis*. [8] Cone of anthers from the same with one of the stamens bent down in the direction of the arrow, and a little pollen escaping in consequence. [9] Stamen with tooth-like handle on its filament. [10] Diagram of transverse section of the style and anthers of *Borago*; the shaded portions are the style and the connectives of the five anthers, the dotted portion is the pollen. [7] natural size; the rest of the figures × 2 to 5.

of pollen to descend upon itself. Usually very small quantities of pollen fall at a time. As soon as the proboscis is withdrawn the anthers are replaced in virtue of their elastic filaments, and the same process may be repeated again and again. The insects break into the flowers at various spots; in Heaths (*Erica*) the proboscis is usually introduced through the apex of the cone of anthers, in Borage (*Borago officinalis*; see fig. 278[7]) at its base. The latter plant is visited by hive- and humble-bees which, alighting on the nodding flowers from below, fasten on with their fore-legs, so that their head and proboscis is brought on to a level with the base of the cone, whilst the hind part of the body is arched under its apex. The insect holds on in this position by a peculiar tooth-like appendage of the filament (see fig. 278[9]), and with this as a handle pulls the anther of that stamen away from the rest, causing a break in the cone out of which the pollen falls on to the abdomen of the insect as it sucks the honey. In the flowers of several *Boragineæ*—Comfrey (*Symphytum*) and *Cerinthe*, for example—there are peculiar scales, furnished with sharp prickles, alternating with the anthers (see figs. 278[4, 5, 6]), and placed in such a position that insects are afraid to insert their

probosces except at the apex of the cone of anthers, and in consequence the head alone and not the abdomen is, in this case, besprinkled with pollen. In *Soldanella* (figs. 278[1] and 278[2]) the apex of each anther is produced into two little processes. Insects come against them as they enter the flower, with the result that pollen is scattered out of the anthers. Several of the wonderful contrivances which were described on p. 271 as occurring in connection with stamens fashioned like sugar-tongs are also present where the conical arrangement of anthers prevails; and we need not, therefore, discuss the latter at greater length. The only case left requiring special attention is that of the Violet and Pansy (*Viola*, fig. 279[1]). Unlike the foregoing, the flower in this case is zygomorphic and has its mouth directed sideways, and moreover, the manner in which the anther-cavities, which are full of floury pollen, are moved by insects is peculiar. The cone of anthers is set over the lowest petal, which is prolonged at the back into a spur containing honey. In order to suck the honey an insect must push under the cone and run its proboscis along the channel of the spurred petal. But here it encounters the thickened extremity of the hooked and deflexed style, which it cannot avoid touching and shifting a little. The five stamens forming the cone are closely adherent to the style, so that any displacement of the latter affects them also, and the moment this happens the proboscis of the intruding insect is besprinkled with pollen from the dislocated cone of anthers.

DEPOSITION OF POLLEN.

The pollen which has been taken from one flower has to be deposited in another by honey-sucking insects and birds. How, when, and where the deposition occurs is of great importance, as the transference is in reality the first stage in the series of events leading to fertilization. The stigma is the destination of the pollen, and the right moment for deposition is as soon as the stigma is able to hold fast the pollen which is brought to it. If the pollen is not deposited on the stigma but on some other part of the flower, or if the stigma be dry and shrivelled, and not able to retain the pollen when deposited on it, it is as much wasted as if it had fallen on to the ground or into the water. Hence not only the time and place of deposition, but also the state of the stigma determine exactly the conditions for the success of the transference of the pollen.

If the pollen is scattered on the back of the insect the stigma must come into contact with its back; if it has adhered to the proboscis, the insect must stroke the stigma of the newly-visited flower with its proboscis; if the under surface of its body is covered with pollen, then the stigma will be placed at the bottom of the entrance to the flower, so that the insect must stroke it with its belly. Obviously, then, an insect, whether abstracting or depositing pollen, will follow approximately the same course in the flower, and that position of the anthers most suitable for the shedding of the pollen will, on the whole, be the position most suitable for the stigma to assume in receiving pollen. It might, therefore, have seemed more natural

to describe the two processes of abstraction and deposition of pollen together. Both have already been referred to, but a thorough description would have greatly encroached on the account of the transference of the pollen by animals reserved till now, and so it seems more natural to treat the deposition of pollen more particularly here, while connecting it with the processes described above as occasion requires.

In the last chapter, when describing the change of position of anthers and stigmas, it was especially noted that in the flower of the Grass of Parnassus (*Parnassia*; see fig. 267 [4] p. 249) one anther after another placed itself in the centre of the flower, because the road to the honey ran through that part, and the sucking-insects were therefore obliged to remove the pollen from the anther standing in their way. But each anther in turn, as it stands in the centre, covers the stigma which surmounts the egg-shaped ovary, and as long as this is the case, the pollen from another flower cannot be deposited there. It is necessary that the last anther of the series, after giving up its pollen, should move out of the way in order that the stigma may be accessible. This actually occurs; the stigma alone is now to be seen in the place where the five anthers have successively appeared, and when other insects come to suck up the honey, the pollen they bring with them from other flowers is deposited on the stigma. The same sort of thing happens in *Funkia*, *Centranthus* and *Impatiens*. In the flowers of *Impatiens*, the anthers form a kind of cap which covers the stigma so as to hide it completely when the flower first opens. Only when the cap becomes loose and falls off is the stigma exposed, standing in the place formerly occupied by the anthers. In these cases the position taken up by the stigma at the commencement of flowering is not usually altered, so that it meets the pollen-laden insect in the exact place where the anthers formerly stood. In order to attain this end, however, the styles of most Saxifrages (e.g. *Saxifraga bryoides, cuneifolia, Geum, rotundifolia, stellaris*) as well as the stigmas of many Gentians, and especially those in the revolver-flowers of the Caryophyllaceæ undergo an alteration of position. Originally, the stigmas of these flowers were placed together in the centre, and the pollen-bearing anthers stood in a circle round them; but, after the anthers have fallen and their filaments have shrivelled up, the style splits, that is to say, the stigmas separate from one another and diverge, taking up the position formerly held by the anthers when liberating their pollen.

The styles of Labiatæ undergo still more marked movements, as, for instance, in the Sage (*Salvia glutinosa*), a representative of this order. When the flower first opens only the end of the style projects as a simple point from the edge of the upper lip (see figs. 271 [1] and 271 [2], p. 262, the right-hand flowers). In this stage the humble-bees, entering the flowers, only carry off pollen, and do not touch the top of the style. Later, the style bends down like a bow, and its branches, at first folded together into a single point, separate and place themselves in front of the entrance to the flower, so that the approaching visitors—the humble-bees—must leave on them the pollen they have brought from other and younger flowers (see

fig. 271 [2], left-hand flowers). A very noticeable change of position of stigmas and anthers is also observed in flowers of the *Gladiolus*, the Hellebore (*Helleborus*), the narrow-leaved Willow-herb (*Epilobium angustifolium*), various species of the genus Honeysuckle (*Lonicera alpigena, nigra, Xylosteum*, &c.), also in the Figwort (*Scrophularia*), species of the genus *Penstemon* and *Cobœa*, and finally in numerous Solanaceæ, as, for example, in the Deadly Nightshade (*Atropa*), the Henbane (*Hyoscyamus*), *Scopolia*, and the Mandrake (*Mandragora*). Looking into the newly-opened flower of the Mandrake (see fig. 279 [8]) we see the spherical, sticky stigma close below the entrance and exactly in the centre. The anthers, surrounding it in a circle, are still unopened and placed against the inner wall of the corolla. Since the mouth of the flower at this time is only slightly open, the stamens are scarcely seen. Two days later the appearance of the same flower is greatly altered. The style, bearing the stigma (now pollinated), has bent sideways and impinges on the inner wall of the corolla, the anthers are pushed towards the middle of the now widely-opened mouth, are covered with pollen, and have thus changed places with the stigma (see fig. 279 [9]). In the flowers composing the umbels and capitula of many Umbellifers, Scabiouses, and Composites, the anthers and stigmas may be said to change places in a certain sense, since the stigmas do not mature until the neighbouring stamens have shrivelled up, or their anthers have fallen off. In the heads of many Dipsaceæ (*Cephalaria, Succisa*), and the head-like umbels of the *Eryngium*, at first only pollen-covered anthers are seen in all the flowers, and later only the stigma-bearing styles. The insects carry the pollen away in masses from these inflorescences, so it is obvious that the deposition must occur in the same manner, *i.e.* that an insect smothered in pollen, alighting on an inflorescence with numerous stigma-bearing styles, and indulging in a series of lively gyrations attaches its load in a few seconds to dozens of the sticky stigmas.

It is hardly necessary to state in detail that the small-pointed thorns, stiff bristles, and other similar structures by which insects are shown the way into the flower have the same significance for the deposition of pollen on the stigma as for its removal from the anthers, and we can now merely refer to the descriptions on pp. 250, 271, and 275. Only one other contrivance especially connected with the deposition of pollen on the stigma, which acts as a remarkable sign-post, need be mentioned here. In the flowers of many Cruciferæ, *e.g.* those of *Kernera saxatilis*, whose first and last stages of development are shown in figs. 267 [8] and 267 [10], p. 249, the petals at the time of opening are still small, stand erect, or are even somewhat inclined inwards, almost touching the large stigma which nearly fills up the entrance to the flower. Insects wishing to suck the honey at the base of the flower are obliged by this position of the petals to push their probosces down close by the stigma. Should the proboscis have been loaded with pollen in other flowers, this will be inevitably deposited on the stigma. Later, when the stigma is withered, and the floral-leaves have enlarged, the whole flower becomes inflated, the floral-leaves becoming concave inwardly, the pollen-covered anthers become visible and accessible; and now when an insect directs its proboscis to the base it no longer touches

the stigma, but brushes off the pollen from the anthers. The same arrangement is repeated with but little deviation in the flowers of the Asarabacca (*Asarum*). The opening of the perianth in this flower begins with the appearance of three fissures between the three perianth-lobes, and these serve as entrance-gates for the small flies seeking access to the interior of the flower (see fig. 279 [12]). The stigmas which are to be pollinated are close below the three fissures, and the insects using

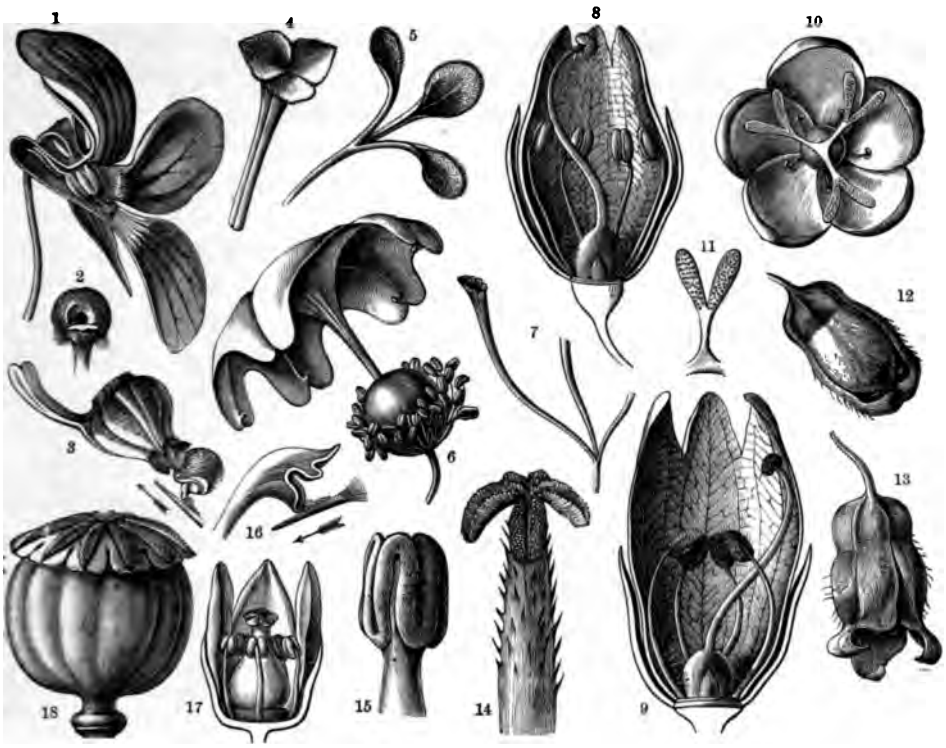

Fig. 279.—Arrangements for the Retention of the deposited Pollen.

[1] Flower of the Violet (*Viola odorata*); part of the corolla cut away. [2] Capitate end of the style of this flower seen from underneath. [3] Pistil of the Violet surrounded by the cone of anthers; pollen is deposited on the small lip of the capitate stigma by the proboscis passing in the direction of the arrow. [4] Stigma of the Narcissus (*Narcissus poëticus*) with finely toothed margin. [5] Stigma of Gladiolus (*Gladiolus segetum*) with ciliated edges. [6] Pistil of *Sarracenia purpurea*; the ovary surrounded by the stamens. [7] Funnel-shaped stigma of the Crocus (*Crocus sativus*); one of the three stigmas only remaining. [8] Flower of the Mandrake (*Mandragora vernalis*) in the first stage of blossoming. [9] The same in the later stage of blossoming. Part of the corolla and calyx cut away. [10] Flower of the Sundew (*Drosera longifolia*) seen from above. [11] Part of the sticky papillose stigma of the Sundew. [12] Flower of the Asarabacca (*Asarum Europæum*) in the first stage of blossoming. [13] The same flower at a later stage. [14] Stigma of *Rosmeria*. [15] Stigma of *Opuntia nana*. [16] Stigma of *Thunbergia grandiflora*; pollen is deposited on the lower lip by a proboscis passing in the direction of the arrow. [17] Flower of *Azalea procumbens*; portions of the calyx and corolla cut away. [18] Pistil of the Opium Poppy (*Papaver somniferum*). [6] and [12] natural size; the others somewhat enlarged.

them as entrance-gates must of necessity pass over the stigmas. If they come laden with pollen from an older flower they cannot avoid leaving a portion behind on the stigmas. Later, when the stigmas are pollinated, the three perianth-lobes separate at the tips also, where they have hitherto been joined together (see fig. 279 [13]). It is then no longer necessary that the insects should be shown the way to the stigmas.

No less important than the position of the stigma and its relation to the rest of

the flower is its capacity for retaining the pollen brought to it. As might be expected, flowers which are visited by insects agree but slightly in this respect with those which are wind-pollinated. In all the instances where the pollen collected by insects or birds has to be brushed off in adhesive crumbling masses, delicate feathery stigmas, such as those of Grasses and many other plants which receive powdery pollen by wind agency, would be of no use; but to the former, stigmas possessing projecting edges, bands, and lobes, on which the insects as they pass must leave their pollen, are better adapted. Usually close to the projecting edge there is a depression which is filled with the deposited pollen. Thus, for example, the style of *Thunbergia* (see fig. 279 [16]) ends in a funnel-shaped stigma whose edge projects on one side like a shovel. When an insect strikes against this stigma on entering, the pollen is received by this shovel and is at once deposited in the funnel-shaped

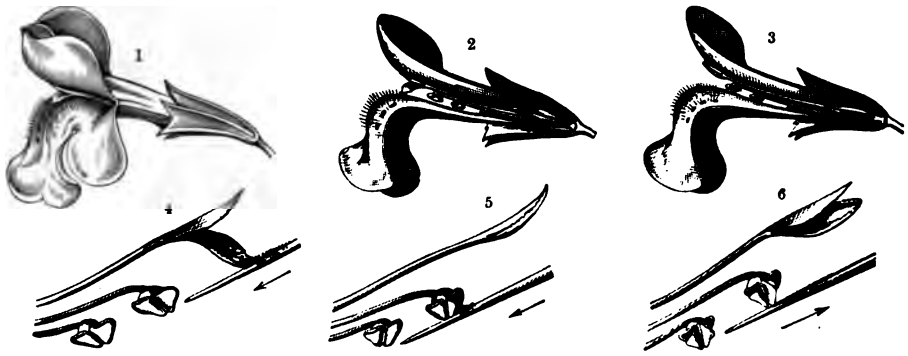

Fig. 280.—Deposition of the Pollen.

[1] Flower of the Monkey Flower (*Mimulus luteus*). [2] The same flower cut in half lengthwise with open stigma. [3] The same flower with closed stigma. [4] Pollen is deposited on the lower lip of the stigma by a proboscis passing in the direction of the arrow. [5] The stigma has closed in consequence of the stimulation: the proboscis passing in the direction of the arrow opens the closed anthers and loads itself with pollen. [6] The lower lobe of the stigma is only slightly raised so that it does not come into contact with the proboscis which is being withdrawn in the direction of the arrow, and consequently the pollen adhering to it does not reach the stigma. [1], [2], and [3] natural size; the others somewhat enlarged.

depression. Insects which push their probosces into the flowers of the Violet (*Viola*) inevitably strike against a little flap projecting from the lower side of the capitate stigma (see figs. 279 [1, 2, 3]), and when the proboscis is covered with pollen this is left adhering to the inner side of the lobe. When the insect withdraws its proboscis the lobe is pressed back against the stigmatic head, and thus the recently received pollen is pushed into its cavity. The flowers of Irises possess stigmas with the shape and colour of petals. They are bilabiate at their free end (see figs. 265 [1] and 265 [2], p. 246). The upper lip of the stigma is curved, fairly large, and split into two points, the lower lip is thin and forms a narrow membraneous lobe spread out transversely. The path traversed by the humble-bee in obtaining the honey passes under one of the bilabiate stigmas, and when it comes laden with pollen from another flower it pushes down the thin flap of the lower lip, so that the pollen is brushed from its back and deposited between the two lips. Many Scrophulariaceæ and Lentibulariaceæ (*Catalpa, Mimulus, Rehmannia, Torenia,* and *Utricularia*), of which the Monkey-flower (*Mimulus luteus,* see figs. 280 [1, 2, 3]), may serve as a type,

have bilabiate stigmas which exhibit sensitive movements. When the pollen is deposited by an insect on the lower lip of the stigma, which stands in its way as it enters (280 [4]), the two lips immediately close together like the leaves of a book (280 [5]), and thus the pollen is carried to that part of the stigma where it undergoes further development. When the insect withdraws its proboscis there is no chance of the pollen which it is taking from the anthers getting into the interior of the stigma, since the stigma is still shut up and no longer stands in the way of the insect (280 [6]). The stigma of *Mimulus luteus* remains closed after being stimulated with a needle for about five minutes; when it again opens, the lower lip resuming its former position, it may be again closed if further stimulated. In other species of the genus, as also in *Martynia* and *Catalpa*, the same phenomenon is observable. None of the previously-mentioned plants appear to keep their stigmas closed more than two minutes. This repeated opening of the stigma is very important in case the first insect visiting the flower should have brought no pollen with it. Since the stigma opens again it has apparently some expectation of a second visit. Should this also be unsuccessful it may open a third time. The opening and closing usually continue until at length an insect deposits pollen on the stigma. When this happens the stigma, though opening yet again for a brief period, remains permanently closed so soon as the influence of the pollen is felt.

The contrivances described above are based on the fact that the pollen stroked off the visiting insects by the projecting edges, bands, and lobes, is conducted from them to the portion of the stigma adapted to receive it. To this first group of contrivances for retaining pollen may be added another where the insect on entering into the base of the flower leaves the pollen it has brought on the papillose, superficial cells of the stigma. This occurs, for example, in the flowers of Malvaceæ and Caryophyllaceæ, the styles of which are studded with long tube-like papillæ; they act like brushes. In the flowers of the Rock-rose (*Helianthemum*), and in those of the Day-Lily (*Hemerocallis*), long papillæ are grouped paint-brush-wise on the capitate stigma, but most frequently the trimming of very numerous long and crowded papillæ has the appearance of velvet, and such stigmas are termed "velvety" by descriptive botanists. The genera *Erythræa*, *Daphne*, and *Hibiscus* may be mentioned as well-known plants with velvety stigmas. In many plants the stigmatic papillæ are but slightly prominent, the surface appearing rough, irregular, or granulated. If the flowers are crowded, and the deposition of pollen occurs simultaneously on numerous stigmas, these are usually linear or only beset with papillæ on one side, as in *Cephalaria*, or clothed all over, as in *Armeria*, but always so formed and placed that the insect moving over the flower-head may rub off its pollen as easily and quickly as possible on to the stigmas. In those plants where the stigma rising in the middle of an erect, shallow flower is used as a resting-place by the insect, either the whole surface is thickly beset with papillæ (*e.g.* in *Roemeria*, fig. 279 [14]), or they are arranged in the form of rows distributed in radial lines, as in the Poppy (*Papaver*, fig. 279 [18]). It frequently happens that the papillæ only border the edge of the stigma, resembling eyelashes on an eyelid,

or the teeth of a comb. This is particularly the case if the stigma is lobed, the lobes being fairly large and spoon-shaped, cup-shaped, or like a funnel, and if the insect on entering only touches the edge of the stigmatic lobes with the pollen-laden part of its body. This is the case, for example, in the flowers of many Gentians, Narcissi, Gladioli, and Crocuses (e.g. *Gentiana Bavarica*, *Narcissus poeticus*, *Gladiolus segetum*, *Crocus sativus*; *cf.* figs. 279 [4, 5, 7]).

Fig. 281.—Evening Primrose (*Œnothera biennis*). (After Baillon.)

The pollen, when deposited, is held between the papillæ of the stigma like dust on velvet pile or on a brush or comb; nor is it absolutely necessary that the stigmatic papillæ should be sticky, though, of course, the power of retention is thus obviously increased. Some stigmas are beset with transparent papillæ, and at the same time are rendered very sticky by a layer of fluid secreted by the surface cells of the stigma, as, for example, in the Sundew (*Drosera*; *cf.* 279 [10] and 279 [11]). But such cases are rare on the whole. Usually the velvety stigmas and those beset with long papillæ are not sticky, the viscosity being restricted to wart-like and granulated stigmas. Examples of plants with very sticky stigmas are furnished by the Umbelliferæ, the Rhododendrons, Bearberries, Ericas, Whortleberries and Cranberries, Winter Greens and Polygonums, the Deadly Nightshade, and Bartsias. A sticky stigma often terminates a thin threadlike style either as a small disc or head, and is the more conspicuous on account of the glitter of its sticky coating than because of its size. In the flower of the Mahogany-tree (*Swietenia Mahagoni*; see fig. 282 [3]) it has the form of a disc, in *Azalea procumbens* (see fig. 279 [17]) it is slightly convex with five projecting ridges radiating from the

centre, in the Prickly Pear (*Opuntia*; see fig. 279[15]) it forms a sinuous fleshy swelling which winds about the end of the style, whilst in the Evening Primrose (*Œnothera*; fig. 281) it is composed of four fleshy lobes arranged in a cross. It is noticeable that sticky stigmas occur most frequently in plants whose pollen is liberated from the sprinkler-like anthers as flour or dust. Such flowers also, the pollen of which consists of quartets (tetrads) of cells surrounded and entangled in delicate threads, are characterized by very sticky stigmas (*cf.* fig. 219[2], p. 101). In most of the plants mentioned above the pollen adheres so firmly to the stigma at the moment of contact that it cannot be removed even by blowing or vigorous shaking. Many of the sticky stigmas remind one of limed twigs, especially as the sticky layer which produces the adhesiveness is exposed to the air and yet does not dry up, but remains sticky and viscous like bird-lime for several days.

In many instances the stigma does not become sticky until the stigmatic tissue is capable of inciting the pollen-cells which come in contact with it to put out pollen-tubes. The stigma of *Cephalaria alpina*, one of the Dipsaceæ, is very remarkable in this respect. Shortly after the corolla has opened, the stigma appears to be completely matured, and as if capable of retaining pollen. But this is not really so. Any pollen placed on it immediately slides off its smooth surface. Not until two days later when the stigmatic tissue has become covered with a delicate layer of sticky fluid, scarcely visible to the eye, is the pollen held fast, and at once puts out pollen-tubes which penetrate into the tissue. But, as in so many other cases, it is impossible to generalize on this point, thus in most Umbelliferæ the stigmas are sticky before their tissue is able to influence the pollen in this way. Also, in the flowers of *Allium Victorialis*, the pollen adheres to the stigmas before these are capable of inciting the emission of pollen-tubes, indeed, at the time of attachment the stigmatic papillæ are not even developed. The stigmas of Orchids are sticky some time before the ovules are matured. In these cases the sticky layer has to retain the pollen until the changes have been completed in the deeper stigmatic tissue which will stimulate the pollen to put out its tubes.

It is necessary to give a special description of the manner in which the pollen is deposited on these sticky Orchid stigmas. The stigma of the Helleborine (*Epipactis latifolia*), illustrated in fig. 268, p. 255, has the form of a rectangular table, and is placed opposite the boat-like labellum, which is filled with honey. When a wasp, in licking out the honey, strikes its head against the projecting rostellum at the upper margin of the stigma it adheres for a moment. The two club-shaped masses of pollen which are connected with the rostellum are thus torn out of the loculi of the anthers, and removed by the wasp as it flies away. The wasp now carries the pair of pollen-masses on its head as shown in fig. 268[6]. At first these pollinia stand erect, but after a few minutes they alter their position. In consequence of drying, the masses, composed of adhering groups of pollen-cells, twist and become deflected, and now appear as two thick cushions lying on the front of the head (see fig. 268[7]). This bending is absolutely necessary if the pollen is to be brought by the wasp to the sticky stigma of another flower. If the wasp came with erect pollen-masses to

lick up the honey they would be knocked off by the rostellum, and their aim would either fail entirely or be but partially achieved. But, as soon as the little clubs have bent down over the front of the wasp's head, they are planted by this honey-licking insect exactly on the sticky rectangular stigmatic surface. Each quartet of pollen-cells forms a round or irregularly rectangular ball, and these, connected together by viscous threads, are again grouped so as to form the club-like pollen-mass. When this club is placed on the sticky stigma, all the pollen-quartets which come into contact remain attached, so that when the insect flies away it is much more likely that the sticky threads in the interior of the pollen-mass will be torn than that the pollen adhering to the stigma will be removed again. These two contrivances, so important for the deposition of the pollen on the stigma, viz. the twisting and bending of the originally erect pollen-masses and the tearing of the fine threads which connect the quartets of pollen-cells, occur not only in the Helleborine (*Epipactis*), which has been chosen as an example, but also in many other Orchids which adorn our woods and meadows—especially in the genera *Orchis*, *Gymnadenia*, and *Habenaria*. In the *Epipogium* (see fig. 257, p. 226) the floral contrivances are rather different. Each pollen-mass is chained on one side by the thick strand which leads to the sticky rostellum (fig. 257 [11]). When these masses are torn from their hiding-place by a humble-bee (257 [13]) they bend round, and now hang on their supports like two cherries on their stalks. In this way the structure, torn from the anther, becomes somewhat elongated—an important change—since it renders it possible that the clubs should reach the stigma in the next *Epipogium* flower visited. In this plant the stigma stands above the rostellum, and the pollinia can only be pressed by flying humble-bees against the stigma if they have long stalks.

Each of these contrivances shows afresh how exact must be the correlation of all the organs which participate in the transference of pollen, and how well they must be regulated if the success of the flower is to be ensured. The alteration of a millimetre in the position of the stigma will prevent the pollen being deposited on the right place and the consequent fertilization. In many cases a still slighter alteration would be hurtful. In some plants only a very limited area of the stigma is able to incite the pollen to emit pollen-tubes. In Asters, as will be shown more in detail presently, it is only a narrow border at the edge of the minute stylar branch, and in many Labiatæ it is only the tip of the lower branch of the stigma on which pollen can be deposited with successful results. *Sarracenia purpurea* possesses one of the largest stigmas. It has the form of a sunshade of 3·5 cm. diameter, with five indented lobes round the edge, and the margin of each lobe is furnished with a small tooth on the inside (see fig. 279 [6]) These teeth alone are fitted to receive pollen, and if the term stigma is to be restricted to the tissue on which the pollen can eventually develop and put out pollen-tubes, it will only refer in *Sarracenia* to these five tiny teeth. The same is true of *Physostigma venenosum* (see figs. 282 [1] and 282 [2]) whose bladder-like stylar termination, described as the stigma, is only capable of real pollination over a small part beset with papillæ. It should also be noted here that the papillæ which are developed on the outer side of the stylar

branches in Compositæ, and which at first sight might be mistaken for stigmatic papillæ, do not deserve this appellation. Their function is only to sweep the pollen out of the anther-tube, and their significance will be repeatedly spoken of later in the chapter devoted to autogamy.

The deposition of pollen on the stigma is followed not only by alterations in the pollen-cells and in the stigmatic tissue, but also in other parts of the flower, especially the corolla. The visible changes in the stigma are the withering, shrivelling, and turning brown of its superficial cells. In those plants described above, on

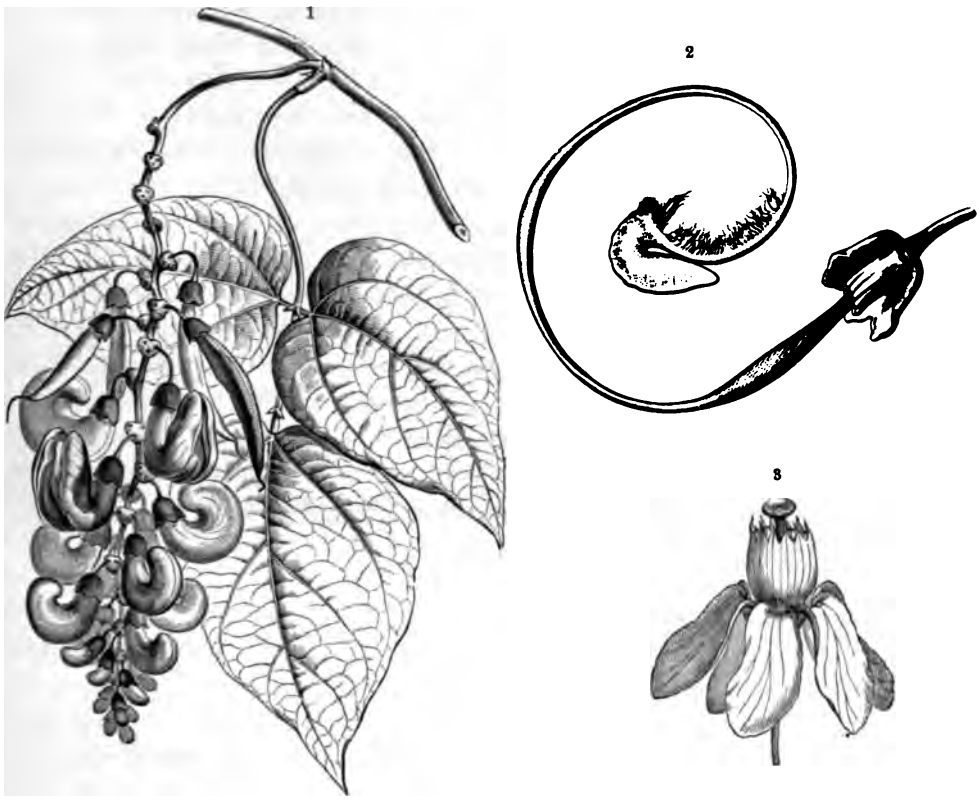

Fig. 222.—1 *Physostigma venenosum.* 2 Pistil of this plant, removed from the flower; magnified. 3 Flower of *Swietenia Mahagoni.* (After Baillon.)

whose sticky stigmas the pollen is not immediately stimulated to send out pollen-tubes, weeks sometimes elapse before these alterations occur; in others, however, they are to be observed in a few hours. Solanaceous plants are very noticeable in this respect, especially *Nicandra physaloides,* and the Deadly Nightshade (*Atropa Belladonna*). An hour after pollen is deposited on the sticky stigma, it begins to wither and turn brown, and the whole style alters and drops off the ovary. Here, then, the pollen-tubes must have been emitted as soon as the pollen-cells came in contact with the stigmatic tissue, and they reach the ovules in the interior of the ovary within a few hours.

The changes which occur in the petals are even more noticeable. As soon

as the stigma is withered they begin to wither also, or they become detached from the flower and fall off. The withering of the petals occurs in very many ways. They lose their turgidity, shrink up, occupy less space, and at the same time change their colour. A change takes place in the petals of most flowers which last only a day, a change similar to that which occurs in foliage-leaves which have passed through a sharp night frost in autumn and then been exposed next day to the sun—*i.e.* they exude water from their tissue and become pulpy and look as if they had been squashed or boiled. The corollas of some Papilionaceæ, especially several species of the Clover genus (*Trifolium*), dry up and rapidly become like withered leaves. The mean between these two instances is furnished by those numerous plants whose flowers become limp, shrink up somewhat, bend over, and then when withered fall off, as, for example, in most Cruciferæ, Valerians, and Compositæ. The petals in withering often assume the position which they occupied originally in the bud. Thus, for example, the tongue-shaped flowers of the Goat's Beard (*Tragopogon*) roll together into a tube on withering, and thus have the same appearance as just before blossoming. Of course this is not always the case, for the tongue-flowers of *Bellidiastrum* and of most Asters roll spirally outwards when they fade, those of *Hieracium staticefolium* spirally inwards, and it is not rare for fading, drying, and discolouring petals to undergo corkscrew-like torsions. The connection between the withering and the discoloration which accompanies it has already been mentioned (p. 222). In many plants it happens that petals drop from the flower either singly or all together after the deposition of pollen on the stigma without having previously withered at all. Examples are furnished by Roses, Almonds, Primulas, and Fuchsias.

It has been repeatedly shown by researches instituted for the solution of the question that the sudden withering and falling of the petals is really dependent on the deposition of pollen on the stigma, *i.e.* on the penetration of pollen-tubes into the stigmatic tissue. If of two flowers which open simultaneously one is provided with pollen and the other is shielded from it, or rather if the stigma of one flower is purposely pollinated while the other is guarded from the deposition of pollen, the latter will last longer and will not fall as soon as the former. In two blossoms of a Flax (*Linum grandiflorum*), which opened at the same time and were treated in this way, the corolla remained 35 hours on the flower whose stigma was pollinated, but 80 hours on the other flower whose stigma had received no pollen. Of two flowers of *Anagallis Philippi* the corolla fell in four days from the one which had been pollinated, but remained for six days on the flower whose stigma had been protected from pollen. In a plant of *Mammillaria glochidiata* the flowers which were pollinated appeared pulpy and permanently closed two days before those whose stigmas remained free from pollen. Orchids as cultivated in hot-houses offer a very well-marked example of this same property. Normally these flowers are free from insect-visits in the hot-house and their flowers remain fresh for many

days, and in some instances for weeks. If, however, the stigmas of these same plants be artificially pollinated, a quick collapse of their showy perianths is observed. If the view that the gaily-coloured corollas act primarily as allurements to insects which visit flowers and transfer pollen require strengthening these results are certainly found to be in accordance. As soon as the end is gained, *i.e.* as soon as the stigma is pollinated, the further allurement of insects is unnecessary; the petals therefore immediately cease working, fall off or wither, and are no longer divergent—in a word, they have ceased to act as an allurement to insects. This phenomenon can only be explained by supposing that the changes produced in the tissues of the stigma by the developing pollen-grains take effect in ever-widening circles which at length reach the petals, and that by what we may term the stimuli, transmitted from the stigmatic tissue and the ovary to the corolla, a sudden separation between the petals and the rest of the flower and an equally sudden alteration in the turgidity of the petals are brought about.

It only remains to be mentioned that the early withering and fall of the petals of those flowers which are pollinated soon after opening has a counterpart in the phenomenon of the long duration of double flowers. Double flowers, in particular those whose stamens and carpels have been transformed into petals, remain fresh two, three, even eight days longer than the normal single flowers of the same kind, as may be seen, for example, in Pelargoniums, Tulips, Pinks and Stocks.

THE CROSSING OF FLOWERS.

While Goethe was staying at Carlsbad a young gardener every day brought him a bunch of flowering plants from the visitors assembled at the waters and undergoing the cure. Both men and women were greatly interested in ascertaining the names of these plants with the assistance of the writings of the Swedish botanist Linnæus, whose fame had at that time spread far and wide. This searching for names was called the "naming" or "determining" of plants, and it was prosecuted with great zeal by dilettanti as a sort of puzzle-game and as a pleasant, stimulating pastime. Even in professional circles Linnæus found a recognition which has rarely been accorded to a contemporary. His method had taken the whole world by storm, and his "system" was everywhere in the ascendant. Of course individual voices were raised against the new teaching, chiefly indeed from the dilettanti. Goethe relates that many of the Carlsbad visitors designated the pursuit of the knowledge of the Vegetable Kingdom according to the Swedish botanist as senseless play which satisfied neither the understanding nor the imaginative faculty, and could relieve no one of ennui. Evidently Goethe also had perceived the weakness of the Linnean method. Besides, he was not concerned with counting or numbers nor the distinction of forms founded on insignificant points; he was not interested in the differences of plants, but rather in what they had in common and in what bound the

Vegetable Kingdom into a many-membered whole. It is therefore obvious that he could never have felt much enthusiasm for the Swedish botanist.

But, strange as it may sound, that which Goethe regarded as the weak point in the Linnean system was, on the contrary, its strength. The very fact that counting afforded a safe path through the apparent chaos of plant-forms, that by means of counting the floral parts the possibility was afforded of attaining to a short and intelligible classification; and not least, the persistent adherence to the principles laid down fascinated both lay and professional men. These same good points explain why even many quite recently issued works (tourists' pocket-floras and the like) retain the Linnean system when their object is to facilitate a speedy reference of a plant to its position amid the plexus-like ramifications of the phylogenetic tree. Later on we shall have an opportunity of investigating the value of the different plant-systems from an historical standpoint. Here the Linnean system claims our attention solely on the ground of the division of the stamens and pistil, *i.e.* of those organs in which the two kinds of sexual cells are formed. The results of the researches into the divisions of these organs in which the fertilizing and receptive sexual cells, *i.e.* the male and female cells are developed, form the foundation of the Linnean system and afford the most important marks for the division into the so-called Classes, of which Linnæus distinguished twenty-four.

The first 20 classes of the Linnean system include Phanerogams, whose flowers are all hermaphrodite, *i.e.* in which each flower of the plant contains both stamens and pistil. Those species whose stamens are all the same length, and are neither joined to one another nor to the pistil, are all in the first 13 classes. Each of these 13 classes is distinguished in the following manner:—

Class.

1. MONANDRIA. A single stamen in each flower; *e.g.* Mare's-tail (*Hippuris*), Indian Shot (*Canna*), *Alpinia* (see fig. 283 [1]).
2. DIANDRIA. Two stamens in each flower; *e.g.* Speedwell (*Veronica*; see fig. 257 [1]), Lilac (*Syringa*; see fig. 283 [2]).
3. TRIANDRIA. Three stamens in each flower; e.g. *Iris* (see fig. 265, p. 246), Valerian (*Valeriana*; see fig. 283 [3]).
4. TETRANDRIA. Four stamens in each flower; *e.g.* Woodruff (*Asperula*), Plantain (*Plantago*), Cornel (*Cornus*; see fig. 283 [4]).
5. PENTANDRIA. Five stamens in each flower; *e.g.* Deadly Nightshade (*Atropa*), Cowbane (*Cicuta*), *Aralia*; (see fig. 283 [5]).
6. HEXANDRIA. Six stamens in each flower; *e.g.* Tulip (*Tulipa*), Lily of the Valley (*Convallaria*), *Gagea* (see fig. 283 [6]).
7. HEPTANDRIA. Seven stamens in each flower; *e.g.* Horse Chestnut (*Æsculus Hippocastanum*; (see fig. 283 [7]).
8. OCTANDRIA. Eight stamens in each flower; *e.g.* Ling (*Calluna*), Spurge Laurel (*Daphne*; see fig. 283 [8]).
9. ENNEANDRIA. Nine stamens in each flower; *e.g.* Bay Laurel (*Laurus*), Flowering Rush (*Butomus*; see fig. 283 [9]).

Fig. 283.—Types of the 1st to 10th classes of the Linnean System.

[1] *Alpinia.* [2] *Syringa vulgaris.* [3] *Valeriana officinalis.* [4] *Cornus mas.* [5] *Aralia Japonica.* [6] *Gagea lutea.* [7] *Æsculus Hippocastanum.* [8] *Daphne Mezereum.* [9] *Butomus umbellatus.* [10] *Phytolacca decandra.* All the flowers somewhat enlarged.

CLASS.

10. DECANDRIA. Ten stamens in each flower; *e.g.* Rue (*Ruta*; see fig. 290), *Phytolacca* (see fig. 283 [10]).

11. DODECANDRIA. Number of stamens not quite definite, 11–20 in each flower; *e.g.* Mignonette (*Reseda*), House-leek (*Sempervivum*), Agrimony (*Agrimonia Eupatoria*; see figs. 285 [1] and 285 [2]).

12. ICOSANDRIA. More than twenty stamens in each flower, situated on the edge of the cup-shaped receptacle (or calyx-tube), their position, therefore, being *above* or *on a level* with the stigma; *e.g.* Rose (*Rosa*), Almond (*Amygdalus*), *Calycanthus*; see fig. 285 [3]) *Chrysobalanus* (see fig. 285 [4]).

13. POLYANDRIA. 20–200 stamens in each flower, springing from the receptacle *below* the pistil; *e.g.* Poppy (Papaver), Lime (*Tilia*; see figs. 284 [1] and 284 [2]) and *Anemone* (see fig. 284 [3])

In the 14th and 15th Classes Linnæus puts all Phanerogams with hermaphrodite flowers in which the stamens are unequal in length.

14. DIDYNAMIA. Includes flowers with four stamens, two long and two short; *e.g.* the Foxglove (*Digitalis*), Snapdragon (*Antirrhinum*; see fig. 284 [6]).

15. TETRADYNAMIA. Includes flowers with six stamens, four long and two short; *e.g.* Mustard (*Sinapis*), Wall-flower (*Cheiranthus*), Bitter-cress (*Cardamine*; see figs. 284 [7] and 284 [8]).

The 16th–20th Classes include all Phanerogams whose stamens are joined in any way either to one another or to the pistil. They are distinguished from one another thus:—

16. MONADELPHIA. The filaments of all the stamens of a flower are joined into a tube; *e.g.* Tamarind (*Tamarindus Indica*; see fig. 284 [9]), Hollyhock (*Althæa*), Mallow (*Malva*), Baobab (*Adansonia*; see fig. 284 [10]).

17. DIADELPHIA. The filaments of the stamens are united and form two groups; *e.g.* Milkwort (*Polygala*), Fumitory (*Fumaria*; see figs. 285 [5] and 285 [6]).

18. POLYADELPHIA. The filaments of the stamens are united and form three or more groups; *e.g.* St. John's Wort (*Hypericum*), *Melaleuca*; (see figs. 284 [4] and 284 [5]).

19. SYNGENESIA. The anthers of the stamens in each flower are joined together into a tube; *e.g.* in *Lobelia*, Hawkweed (*Hieracium*; see figs. 222 [4] and 222 [7], p. 112).

20. GYNANDRIA. The stamens are united with the pistil; *e.g.* the Orchids: *Phalænopsis*, (see figs. 258 [1] and 258 [2], p. 227); *Cypripedium* (see figs. 267 [1] and 267 [2], p. 249); *Epipactis*; see figs. 268 [2] and 268 [3], p. 255); also the Birthwort (*Aristolochia*; see figs. 284 [11] and 284 [12]).

Now come those plants whose flowers are not hermaphrodite or not all hermaphrodite, and these are distinguished in the following way:—

21. MONŒCIA. Flowers monœcious, *i.e.* the flowers which contain only stamens or only pistils, are separated but grow on the same plant, *e.g.* the Maize (*Zea Mais*), the Oak (*Quercus*; see fig. 286); the Castor-oil Plant (*Ricinus*; see figs. 285 [7] and 285 [8]), *Croton* (see figs. 285 [11] and 285 [12]), *Liquidambar* (see figs. 285 [9] and 285 [10]).

22. DIŒCIA. Flowers diœcious, *i.e.* the flowers containing stamens only are found on certain plants, and those with pistils only on other plants; *e.g.* the Willow (*Salix*; see fig. 287).

23. POLYGAMIA. Flowers polygamous, *i.e.* staminate, pistillate, and hermaphrodite flowers are all found either on the same or on different plants, in various ways; *e.g.* the Ash (*Fraxinus*; see fig. 230, p. 138).

24. CRYPTOGAMIA. Includes Non-flowering Plants.

Linnæus described 20 out of the 23 Classes of Phanerogams as hermaphrodite. He considered hermaphrodite flowers generally to be the rule, and thought them more complete than the unisexual. He connected their prevalence directly with the formation of fruit, and believed the presence of stamens and pistils in the same flower could be explained most simply and naturally by the fact that fertilization could be performed much more easily when the receptive and fertilizing organs were in immediate proximity than when they were widely separated, and thus the formation of seeds capable of germination be best ensured. In a word, the idea originated and found expression afterwards as an actual doctrine that fertilization begins in hermaphrodite flowers by the transference of the pollen on to the stigma of the same flower, *i.e.* that the process occurs which we now call *autogamy* or self-fertilization. More recent researches, however, have shown that many plants are only apparently (or pseudo-) hermaphrodite; that stamens and carpels indeed stand close together in their flowers, but that the pollen-grains in the anthers are not properly developed and have lost their fertilizing capacity. In other flowers, regarded as hermaphrodite, the ovules are so altered that they are unable to develop into seeds capable of germination. It has also been shown that plants provided with both unisexual and hermaphrodite flowers, which Linnæus called polygamous and placed in the 23rd Class, occur much more frequently and in much greater variety than was formerly supposed. There is a long series of forms, one limit of which is constituted by plants with truly hermaphrodite flowers, and the other by dicœcious plants. It is impossible, for want of space, to give an exhaustive description of all the members of this series; but since it is important, for the sake of what follows, to obtain as clear an idea as possible of this matter, the chief members of the series at any rate will now be enumerated.

At one end of the series, then, are the bisexual flowers. They always contain one or several stamens besides the ovary. In the ovary are developed the ovules which after successful fertilization become seeds capable of germinating; whilst the anthers of the stamens contain pollen grains which have the power of fertilizing. These flowers are termed *hermaphrodite* and it is desirable to emphasize the expression by speaking of them as truly hermaphrodite flowers.

The unisexual flowers come next. In these only one of the two sets of organs which take part in fertilization is fully matured and able to perform its function. When only the pistil is present, with ovules capable of development, and the stamens do not mature or are entirely absent, the flowers are called female or pistillate; flowers which contain stamens only, with fertile pollen, whose pistil does not mature or is altogether absent, are termed male or staminate. Four kinds of unisexual flowers may be distinguished: (1) Pistillate flowers which appear hermaphrodite. In these pistil and stamens are present, and these flowers therefore seem at first sight to be bisexual. Their pistil contains ovules which can be fertilized and are capable of development, but the cells which are formed in the tissues of the anthers have no fertilizing power. (2) Staminate flowers which appear hermaphrodite. These are the counterpart of the first group. They also contain both

Fig. 284.—Types of the 13th, 14th, 15th, 16th, 18th, and 20th classes of the Linnean System.

1, 2 *Tilia*, whole flower and section of same. 3 *Anemone nemorosa*. 4, 5 *Calothamnus*, whole flower and section of same. 6 *Antirrhinum*, upper lip of corolla showing stamens. 7 *Cardamine pratensis*. 8 The same flower, the petals removed. 9 *Tamarindus*. 10 *Adansonia*. 11 *Aristolochia Clematitis*. 12 The same flower after removal of the perianth. 6, 9, 10, 11 natural size; the others somewhat magnified.

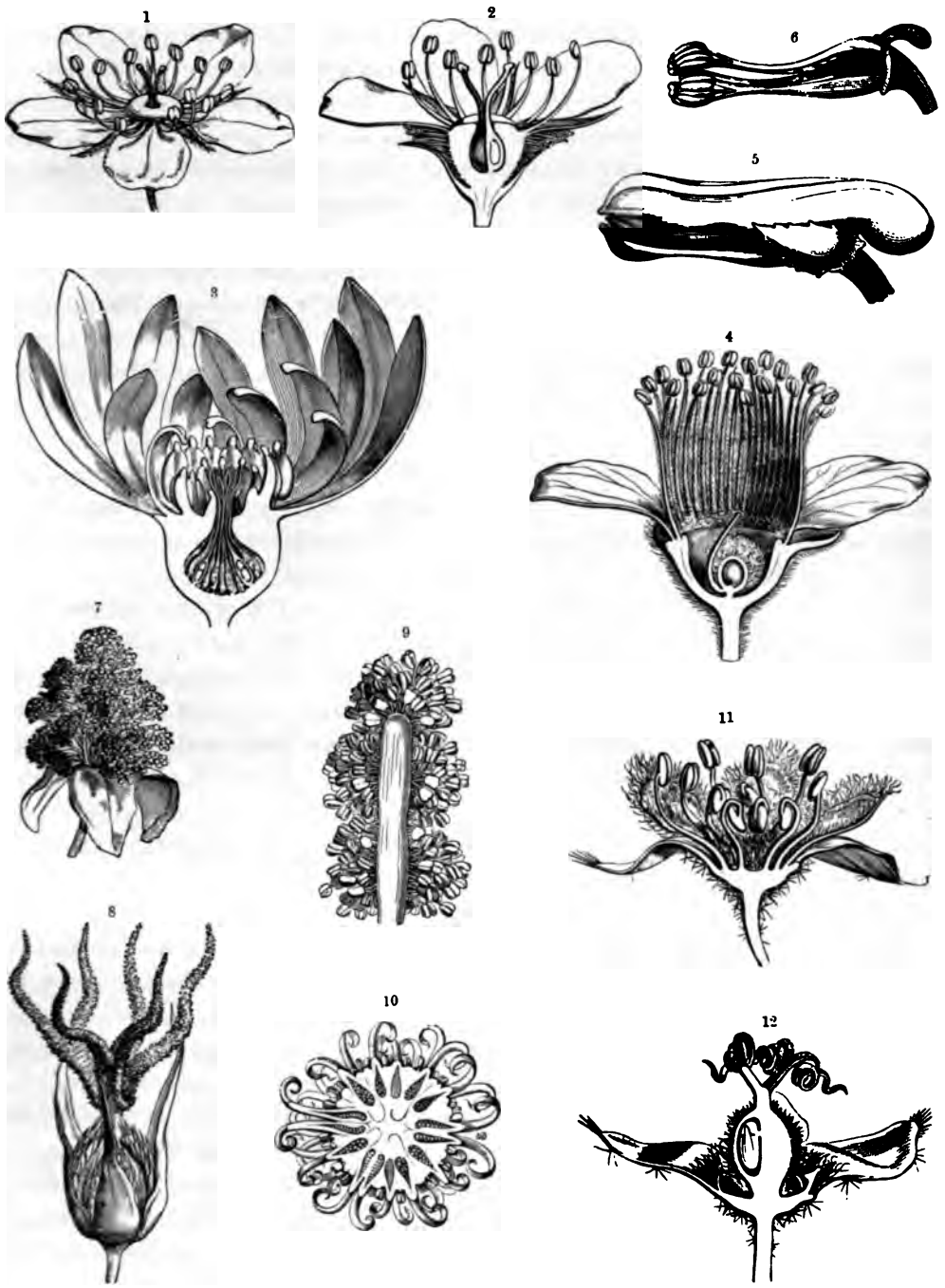

Fig. 285.—Types of the 11th, 12th, 17th, and 21st classes of the Linnean System.

[1], [2] *Agrimonia Eupatoria*, whole flower and section of same. [3] *Calycanthus*, cut through longitudinally. [4] *Chrysobalanus*, longitudinal section of flower. [5] *Fumaria officinalis*, whole flower. [6] The same flower after the removal of the petals. [7] Staminate flower of *Ricinus communis*. [8] Pistillate flower of *Ricinus communis*. [9] Staminate flower of *Liquidambar*. [10] Pistillate flower of *Liquidambar*. [11] Staminate flower of *Croton*. [12] Pistillate flower of *Croton*, both halved. All the figures somewhat enlarged.

stamens and pistil, and so might also be mistaken for hermaphrodite flowers, but closer examination shows that their ovaries do not develop sufficiently to produce fertile seeds. The ovules, and usually the stigmas as well, do not mature, but the pollen in the anthers attains its full power. (3) True pistillate flowers. In these only fertile ovaries are developed, and there is no trace of stamens. (4) True staminate flowers, the counterpart of the third group. They contain stamens whose anthers hold ripe pollen, but their ovaries are quite suppressed.

To the four types of unisexual flowers we shall apply short descriptive names, at once rendering the character of the flower apparent, and saving much needless iteration and confusion. (1) *Pseudo-hermaphrodite female flowers* are the pistillate flowers which appear to be hermaphrodite, similarly (2) *Pseudo-hermaphrodite male flowers* are the staminal flowers which, from the presence of reduced pistils, appear to be hermaphrodite. (3) True *pistillate flowers*, and (4) True *staminate flowers*.

Next to the unisexual come the neuter (sterile) flowers, in which the ovaries and stamens are either altogether absent, the flower consisting merely of petals and sepals, or the sexual organs if present are quite rudimentary and hidden away in the centre of the flower.

The kinds of flower enumerated here are connected together by numerous transitional forms. In the hermaphrodite flowers of the Knawel (*Scleranthus*) two or three of the four stamens are often sterile; they occupy their right position, but their anthers are shrivelled and contain no ripe pollen, only one or two of the stamens being properly developed. Of the eight stamens of the well-known garden-plant *Clarkea pulchella* only the four which alternate with the petals form fertile pollen, while the anthers of the other four are abortive. Sometimes five, six, seven, or even all the anthers are sterile. The Chickweed (*Stellaria media*) has ten stamens arranged in two whorls of five, but it rarely happens that all the anthers produce fertile pollen. Usually those of the five inner and often of a pair of the outer whorl are shrivelled and have no pollen. These instances evidently form good links between the true hermaphrodite and the pseudo-hermaphrodite flowers. The flower-heads of the Burnet (*Poterium polygamum*) consist of pistillate, staminate, and truly hermaphrodite flowers. In the staminate flowers sixteen stamens are formed; the hermaphrodite flowers may contain eight, seven, six, or gradually decreasing numbers down to only one. The other stamens are not even formed, not the slightest trace of them can be found. These flowers may be regarded as connecting the truly hermaphrodite with the pistillate flowers, for if the suppression of stamens be supposed to go still further, so that the last stamen has disappeared, then the flower is no longer hermaphrodite, but has become a true pistillate flower.

The gradations in the class of pseudo-hermaphrodite, pistillate, and staminate flowers are also very varied. The Fuller's Thistle (*Cirsium*), the Flowering Ash (*Fraxinus Ornus*), the Asparagus (*Asparagus officinalis*), the Date-plum (*Diospyros Lotus*), the Vine (*Vitis vinifera*), many Scabiouses, Saxifrages, Valerians, &c., all

develop imperfect flowers, which are liable to be mistaken at first sight for truly hermaphrodite. They have plain well-developed ovaries, and stamens in whose anthers pollen-grains are formed in greater or less numbers; but experiments with this pollen have shown that when deposited on the stigma it emits no pollen-tubes, and consequently the flowers are not in reality truly hermaphrodite, but only apparently so. This is the case in some of the flowers in the panicle of the Horse Chestnuts (*Æsculus* and *Pavia*), in some species of Dock (*Rumex alpinus, obtusifolius*, &c.), and in some of the flowers in the centre of the heads of the Colt's-foot, Marigold, and Butter-bur (*Tussilago, Calendula, Petasites*). They appear hermaphrodite although the ovaries never form fruits with fertile seeds, because their stigmas are not capable of inciting the emission of pollen-tubes in the ripe pollen deposited on them. Again, there are many plants where either the ovaries or the stamens are so reduced that they can only be discovered by careful searching. Some examples of the red Campion (*Lychnis diurna*) have flowers with well-developed ovaries and stigmas, which are capable of fertilization, while their stamens are extremely minute, consisting of triangular bodies scarcely 1 mm. long, which bear a small polished head destitute of pollen instead of an anther. Other plants of this same Campion bear flowers with ten stamens whose long ribbon-like filaments are surmounted by large anthers with fertile pollen, but instead of the ovary there is only a minute knob with two points indicating the stigma. The same thing occurs in the flowers of some Valerians (*Valeriana dioica, simplicifolia*, &c.). The racemes of the Sycamore (*Acer Pseudo-platanus*) exhibit every imaginable gradation from pseudo-hermaphrodite male flowers, with comparatively large ovaries, to those in which the ovaries are reduced or altogether absent. I have mentioned these instances, to which many others might be added, to show that there is no lack of transitional forms between pseudo-hermaphrodite and truly pistillate and staminate flowers; and again, in plants with neuter flowers, especially in many species of the Grape-Hyacinth (*Muscari*), we have gradations from truly-hermaphrodite to neuter flowers. The remarkable structures known as gall-flowers (*cf.* pp. 159, 160) may also be mentioned here. They represent neuter flowers, and occasionally undoubted links are found between them and true pistillate flowers. In spite of these transitional forms, which to some extent break down the limits between the various kinds of flower, it is advisable to retain the names already used for the separate forms, since otherwise it would be impossible to give a general account of the arrangement of the sexes in Phanerogams.

It has been stated above that botanists were formerly content with dividing plants according to their sex into those with hermaphrodite, monœcious, dicecious, and polygamous flowers (*cf.* p. 291). This classification, however, is no longer adequate to the present standpoint of our knowledge. I will now attempt to give an approximate account of the extremely complex conditions which must be considered in this matter, but will keep to the old divisions as far as possible in so doing.

We may place in the first group those plants whose species develop true herma-

phrodite flowers exclusively. Although this group is not so comprehensive as it was thought to be in the time of Linnæus, it is nevertheless the most important, and includes more than a third of all the Phanerogams. The *Alpinia*, Lilac, Cornel, *Gagea*, Spurge Laurel, Flowering Rush, *Phytolacca*, Agrimony, Lime, Anemone, Bitter-cress, Baobab, and *Melaleuca*, all figured on pp. 289, 292, 293, may be mentioned as examples.

Close to these comes a second group of species which bear pseudo-hermaphrodite female flowers as well as truly hermaphrodite flowers, as, for example, *Oxyria digyna* and *Geranium lucidum*.

The third group includes those species whose individuals develop both true hermaphrodite flowers and those which appear to be so, but are really pseudo-hermaphrodite male flowers. Though instances of the second group are rare, the third comprises hundreds of species from widely-different families. Special instances are furnished by the North American Shrubby Trefoil (*Ptelea trifoliata*), the common Bistort (*Polygonum Bistorta*), the Horse-Chestnuts (*Æsculus, Pavia*), some Aralias (e.g. *Aralia nudicaulis*), several species of Bed-straw and Woodruff (e.g. *Galium Cruciata, Asperula taurina*), and many Umbelliferæ. In the last-named the arrangement and distribution of the two kinds of flowers is quite determinate for each genus, and has the closest connection with the processes of pollen-transfer. In *Anthriscus* the umbellate heads of the central umbel contain for the most part true hermaphrodite flowers surrounded by a few pseudo-hermaphrodite male flowers. The heads of the lateral umbels, however, are composed entirely of these staminate flowers. In *Caucalis* the central umbellate heads consist exclusively of pseudo-hermaphrodite male flowers, while the other heads are formed of 2 true hermaphrodite flowers and 4–7 pseudo-hermaphrodite male flowers. In *Astrantia* the large central umbels contain 12 hermaphrodite flowers surrounded by a few pseudo-hermaphrodite male flowers, but the lateral, smaller umbels contain the latter only. *Athamanta cretensis, Chærophyllum aromaticum* and *Meum Mutellina* have in all their umbels a central hermaphrodite flower surrounded by staminate flowers (*i.e.* male pseudo-hermaphrodites), and these in turn are surrounded by true hermaphrodite flowers. All the umbels of *Chærophyllum Cicutaria* and *Laserpitium latifolium* contain short-stalked pseudo-hermaphrodite male flowers surrounded by long-stalked truly hermaphrodite flowers. In the centre of all the umbels of *Turgenia latifolia* are 6–9 pseudo-hermaphrodite flowers which do not radiate, and 5–8 true hermaphrodite flowers, ray-like on the circumference; whilst in *Sanicula europæa* there are three central hermaphrodite flowers in each umbel surrounded by 8–10 pseudo-hermaphrodite male flowers.

In the fourth group each plant bears both truly hemaphrodite and truly pistillate flowers. A large number of Composites come under this heading, of which the Asters may be taken as a type (*Aster, Bellidiastrum, Stenactis, Solidago, Buphthalmum, Inula, Arnica, Doronicum*, &c.). The tubular florets of the disc are truly hermaphrodite in each capitulum, while the tongue-shaped ray-florets are truly pistillate. This division of the sexes also occurs in other Compositæ, of which

the genera *Homogyne* and *Helichrysum* may be taken as typical, where the ray-florets are not tongue-shaped but threadlike. This arrangement is rarely met with except in these Composites. Strangely enough, it occurs in a species of Gladiolus (*Gladiolus segetum*).

The fifth group is made up of species where every plant bears both hermaphrodite and true staminate flowers. For examples we have the so-called White Hellebore (*Veratrum*), the Crown Imperial (*Fritillaria imperialis*), the Snake-root (*Calla palustris*), and numerous Grasses belonging to the genera *Andropogon*, *Arrhenatherum*, *Hierochloa*, *Holcus*, and *Pollinia*.

A sixth group comprises those species in which every plant bears both true pistillate and pseudo-hermaphrodite male flowers, but none that are truly hermaphrodite. In this group are placed the Marigold (*Calendula*), the Colt's-foot (*Tussilago*), and *Micropus*. Here tubular staminate flowers (which are really pseudo-hermaphrodite) occupy the centre of the capitulum, and true pistillate flowers, either tongue-shaped or filiform, occur at the circumference. The Edelweiss (*Gnaphalium Leontopodium*) and the Butter-bur (*Petasites*) also belong to this group. In the two last-named plants, however, the arrangement in the single capitula is of a peculiar kind differing from that in the other Composites mentioned. There are three kinds of individuals of Edelweiss. In one the central head of the whole inflorescence contains only pseudo-hermaphrodite male flowers, whilst in the second form the central capitulum is again formed entirely of pseudo-hermaphrodite male flowers, but in the other capitula these are surrounded by true pistillate flowers. In the third form all the capitula have pseudo-hermaphrodite male flowers surrounded by true pistillate flowers. In the Butter-bur (*Petasites*) all the capitula have pseudo-hermaphrodite male flowers in the centre, and true pistillate flowers around the circumference, but strangely enough the number of these varies from plant to plant. In some plants the pseudo-hermaphrodite male flowers are very numerous, and the capitula contain but few true pistillate flowers and *vice versâ*. These two kinds of plants differ very much in appearance, and the Butter-bur might therefore be easily mistaken for a dicœcious plant.

The seventh group includes all those species in which each plant develops both true staminate and true pistillate flowers, species which have been previously termed monœcious. Examples of this large group are: Oak (*Quercus*; see fig. 286), Hazel (*Corylus*; see fig. 235, p. 147), Alder (*Alnus*; see fig. 228, p. 135), Walnut (*Juglans*; see fig. 184, vol. i. p. 742), Pine (*Pinus*; see fig. 233, p. 144), many Urticaceæ (*Urtica urens*, *Pachysandra*), numerous Aroids (*Arum*, *Ariopsis*, *Arisema*, *Richardia*, &c.), many Palms, a number of marsh and water plants (*Myriophyllum*, *Sagittaria*, *Sparganium*, *Typha*, *Zannichellia*), some Grasses (*Heteropogon*, *Zea Mays*), and, especially, many Euphorbiaceæ and Cucurbitaceæ.

Species belonging to the eighth group have three kinds of flower side by side on the same plant, *i.e.* pseudo-hermaphrodite male and pseudo-hermaphrodite female flowers and true hermaphrodite flowers. Examples are furnished by various Acers (*Acer Pseudo-platanus* and *platanoides*), Sumachs (e.g. *Rhus Cotinus* and *Toxi-*

codendron), Laurels (e.g. *Laurus nobilis* and *Sassafras*), many Docks (e.g. *Rumex alpinus* and *obtusifolius*), the Wall Pellitory (*Parietaria*), and also some Saxifrages (e.g. *Saxifraga controversa* and *tridactylites*).

The ninth group consists of species whose individuals each bear true hermaphrodite flowers along with true pistillate and true staminate flowers. The Ash (*Fraxinus excelsior*; see fig. 230, p. 138) is an example of this group.

Fig. 286.—Type of a monœcious plant.

[1] Oak (*Quercus pedunculata*); pistillate flowers on the upper part of the twig, staminate flowers (in pendent catkins) below. [2] A single pistillate flower of the same plant. [3] Three staminate flowers of the same plant. [1] nat. size; [2] and [3] × 4.

Now come the groups whose species contain two or three kinds of flowers *distributed on two or several plants.*

Species belonging to the tenth group bear true hermaphrodite flowers on one plant and pseudo-hermaphrodite female flowers on another. Examples of this are: numerous Valerians (e.g. *Valeriana montana, Saliunca, supina*), some Dipsaceæ (e.g. *Scabiosa lucida, Knautia arvensis*), many Saxifrages (e.g. *Saxifraga aquatica*), the cultivated Vine (*Vitis vinifera*), many Caryophyllaceæ (e.g. *Dianthus glacialis* and *prolifer, Lychnis Viscaria, Silene noctiflora*), and, especially, very many Labiatæ (e.g. *Calamintha, Glechoma, Marrubium, Mentha, Origanum, Prunella, Thymus*).

In the eleventh group we place those plants which develop true hermaphrodite flowers on one plant and pseudo-hermaphrodite male flowers on another, as, for example, numerous Ranunculaceæ (e.g. *Ranunculus baldensis, Pulsatilla alpina, vernalis, Ranunculus alpestris, glacialis*), many Rosaceæ (e.g. *Dryas octopetala, Geum montanum* and *reptans*), and many species of Vine (e.g. *Vitis sylvestris, macrocirrha*).

The twelfth group comprises those species which bear pseudo-hermaphrodite female flowers on one plant and pseudo-hermaphrodite male flowers on another. This is observed in species of Buckthorn of the section Curvispina (*Rhamnus cathartica, saxatilis, tinctoria*), in various Caryophyllaceæ (e.g. *Lychnis diurna* and *vespertina*), in Asparagus (*Asparagus officinalis*), the Rose-root (*Rhodiola rosea*), the Mountain Currant (*Ribes alpinum*), and the Fuller's Thistle (*Cirsium*).

Fig. 237.—Type of a dicecious plant: Crack Willow (*Salix fragilis*).

[1] Twig with pistillate catkins. [2] Twig with staminate catkins. Natural size.

The Mountain Cudweed (*Gnaphalium dioicum*) and the closely allied species of the same genus, *Gnaphalium alpinum* and *carpaticum*, also belong to this group.

The thirteenth group contains numerous species all bearing true pistillate flowers on one plant and true staminate flowers on another; they were termed *diœcious* by Linnæus. Examples are: *Ephedra*, Cycads, Juniper, Yew, and Ginkgo (*Juniperus, Taxus, Ginkgo*), numerous Sedges (e.g. *Carex Davalliana, dioica*), *Vallisneria* (see fig. 155, vol. i. p. 667), Hemp and Hop (*Cannabis, Humulus*), the Paper Mulberry (*Broussonetia papyrifera*; see fig. 229, p. 137), Dog's Mercury

(*Mercurialis*), some Docks (*Rumex Acetosa, Acetosella*), Sea Buckthorn (*Hippophae*), Poplar (*Populus*), and the Willows, one of which is figured on last page.

The fourteenth group consists of species which bear true hermaphrodite flowers on one plant and pseudo-hermaphrodite female flowers on another, and pseudo-hermaphrodite male flowers on a third plant. Caryophyllaceous plants afford many examples of this group, viz. *Saponaria ocymoides, Silene acaulis, nutans, Otites* and *Saxifraga*. This arrangement is less often met with in Gentians, as, for example, in *Gentiana ciliata*.

A fifteenth group may be added, in which the species have their three kinds of flowers distributed in four ways on different plants, so that they can be divided into four varieties. *Spiræa Aruncus* is typical of this. It produces true hermaphrodite flowers and pseudo-hermaphrodite male and female flowers. The three kinds of flowers are arranged thus: (1) some plants bear only pseudo-hermaphrodite female flowers, (2) others only pseudo-hermaphrodite male flowers, (3) some bear both hermaphrodite flowers and pseudo-hermaphrodite male flowers, and (4) in addition there are yet other plants whose flowers are all hermaphrodite.

To complete this summary it should be mentioned that some species exhibit deviations from their usual distribution of the sexes, although this is not often the case. For instance, plants of the dicecious Nettle (*Urtica dioica*) sometimes occur with both true pistillate and staminate flowers on the same individual. The same thing is occasionally seen in Willows. Most of the plants of the Wild Basil (*Clinopodium vulgare*) in a given locality bear hermaphrodite flowers, but from a few of the flowers on some plants anthers are either partially or wholly absent. Staminate plants of *Vitis cordata* were grown in the Vienna Botanical Gardens and only developed staminate flowers for many years, but occasionally true hermaphrodite flowers appeared as well. Single staminate flowers have been repeatedly observed on the pistillate plants of the dicecious Dog's Mercury (*Mercurialis annua*), and in *Lychnis diurna* and *vespertina* true staminate flowers and isolated hermaphrodite flowers are sometimes found together. Single hermaphrodite flowers occur here and there in the inflorescences of the Castor-oil plant (*Ricinus communis*) among the true pistillate and staminate flowers, and on many plants of *Saponaria ocymoides* true hermaphrodite and pseudo-hermaphrodite female flowers have been seen together with pseudo-hermaphrodite male flowers.

In the light of these results of recent investigation it is evident that the theory expressed in the Linnean System, viz. that the great majority of Phanerogams bear only hermaphrodite flowers, is not confirmed, and that the view held by Linnæus as to the completeness and importance of this type of flower breaks down with it.

But since it is now established that the separation of the sexes in the Vegetable Kingdom is such a widespread phenomenon, it must offer some advantage, and this advantage can only lie in connection with cross-fertilization. By *cross-fertilization* in Phanerogams we mean here the transference of pollen-cells from one flower to

the stigma of another which contains the female sexual cells in its ovary; and we may distinguish between crossing in plants of the *same* and of *different* species. In the former case the pollen of one flower is deposited on the stigma of another flower belonging to a plant of the *same* species; in the latter case the pollen is deposited on the stigma of a flower which is *not of the same* species. Obviously in the latter process, which is also termed *hybridization*, the two flowers are some distance apart. Of the former process there are two varieties, viz. *Geitonogamy* (from γείτων, a neighbour, and γάμος, marriage), when the two flowers are immediate neighbours, growing upon the same plant, and *Xenogamy* (from ξένος, a stranger, and γάμος, marriage), when they are on different plants of the same species.

Although the distribution of the sexes on different plants or in different flowers of the same plant has been indicated as advantageous, even as a condition for the occurrence of cross-fertilization, it must not be supposed that it is the only contrivance for ensuring hybridization, xenogamy, or geitonogamy. It is beyond question that the same result is obtained in true hermaphrodite flowers, *i.e.* that plants whose flowers all contain fertile pollen-grains and ovaries which are capable of development can cross with one another. Of course special arrangements are necessary for this, and the more important of them will be mentioned in the following pages and illustrated by a few examples. In some instances cross-fertilization is unavoidable from the mutual arrangement and position of the two kinds of sexual organs which occur together in a true hermaphrodite flower. If during the whole time of flowering the stigma assumes such a position as to be brushed by an insect which is visiting the flower, but at the same time is so placed that it cannot receive the pollen from the anthers immediately surrounding it, it may be safely assumed that it is adapted to cross-fertilization. This is the case, for example, in the White Lily (*Lilium album*), Day Lily (*Hemerocallis flava* and *fulva*), *Anthericum*, and numerous bulbous plants of the Cape (*Amaryllis*, *Albuca*, &c.) The entrance to these flowers is directed laterally, and the style projects so far beyond the anthers with their sticky pollen that its stigma never receives any of it. On the other hand, when the projecting style is used as a resting-place by flying animals which come laden with pollen from another flower. it is unavoidable that foreign pollen should be deposited on the stigma, and so a crossing results. The same is true of various Boraginaceæ (e.g. *Echium*), Scrophulariaceæ (e.g. *Pœderota Ageria*), Bindweeds (e.g. *Convolvulus sepium, sylvaticus, lucanus*), Caprifoliaceæ (e.g. *Linnæa borealis*), Rhododendrons (e.g. *Rhododendron Chamæcistus*), and Cactaceæ (e.g. *Mammillaria, Echinocactus*). Many flowers whose entrance is directed upwards (e.g. *Lilium bulbiferum, Glaucium luteum, Gentiana Bavarica, nivalis, verna*) show the same condition of anthers and stigmas. In the flowers of the Mezereon (*Daphne Mezereum*) the stigma is not beyond and above the anthers, as in the plants just mentioned, but it forms the termination of the ovary at the base of the perianth-tube, whilst the anthers are situated in the upper part of the tube. Some pollen may occasionally fall from the anthers on to the stigmas in erect flowers, especially when they shrivel

up as the blossom fades, but the majority of Mezereon flowers stand out horizontally from the branches, and in these it is hardly possible for the adhesive pollen to reach the stigmas unaided, although the anthers and stigma are not more than 2 mm. apart. Mezereon flowers are visited so industriously by bees, however, that most of the stigmas are pollinated by strange pollen, and thus manifold crossings are obtained. In the majority of Orchids, too, the pollen is only brought from its hiding-place by insects which hardly ever deposit it on the adjacent stigma, but as a rule transfer it to the stigma of another flower.

Heterostyled plants present a peculiar condition. Many Gentianaceæ (e.g. *Menyanthes trifoliata, Gentiana Rhætica* and *Germanica*), the various species of Bastard Toadflax (*Thesium*), numerous Primulaceæ (e.g. *Androsace, Aretia, Gregoria, Hot-*

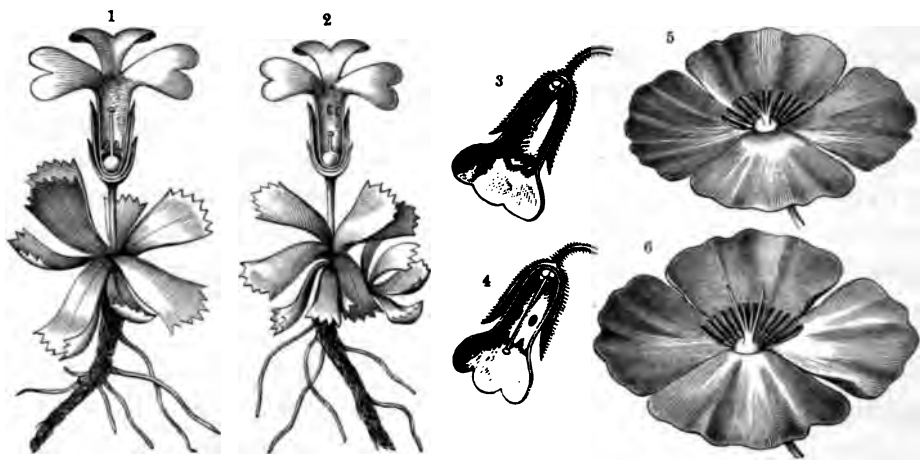

Fig. 288.—Heterostyled flowers.

[1] Plant of *Primula minima* with a long-styled flower. [2] Plant of the same species with a short-styled flower. [3] Short-styled flower of *Pulmonaria officinalis*. [4] Long-styled flower of *Pulmonaria officinalis*. [5] Short-styled flower of *Eschscholtzia Californica*. [6] Long-styled flower of the same plant. All nat. size.

tonia, Primula, see figs. 288 [1] and 288 [2]) as well as many Boraginaceæ (e.g. *Myosotis, Mertensia, Pulmonaria*; see figs. 288 [3] and 288 [4]) and members of other groups, bear flowers with relatively short styles on one plant, the anthers being above the stigma, while, on another plant of the same species, the flowers have all relatively long styles, and the anthers are inserted below the stigma. At the opening of the flowers the stigmas cannot receive pollen unaided either from the anthers above or from those below them. But an insect, which, by inserting its proboscis into a short-styled flower, has brushed against the anthers at the mouth of the corolla-tube, and thus loaded itself with pollen, will deposit this exactly on the stigma of a long-styled flower, should it enter one, since the stigma is just at the same level in the second flower as the circle of anthers in the first-visited, short-styled form. In the same way it is hardly necessary to say that the pollen, which has adhered to the proboscis of a honey-sucking insect half-way up the corolla-tube of a long-styled flower, will be deposited on the stigma which reaches the same level in a

short-styled flower. I shall return to the subject of heterostyly in the next chapter, and will merely say here that there are also plants whose anthers and stigmas present three kinds of arrangement. For example, in the Purple Loosestrife (*Lythrum Salicaria*) the flowers on one plant will have long styles, on another medium styles, and short styles on a third plant; the two whorls of stamens in plants with long-styled flowers are below the stigma; in the medium-styled flowers, one whorl of anthers is above, and the other below the stigma; whilst in the short-styled flowers both whorls of anthers are above the stigma. We should also briefly state here that the *Eschscholtzia*, which usually possesses four styles (figs. 288 [5] and 288 [6]), develops styles of unequal length in its flowers; in some flowers, which are distinguished by their larger circumference, there are two longer and two shorter. The longer styles receive the pollen from other flowers, and are adapted to cross-fertilization, while the shorter styles are pollinated by the anthers standing close beside them (fig. 288 [6]). There are also smaller flowers containing four styles which are all so short that they do not project above the pollen-producing anthers (fig. 288 [5]). We can only briefly touch upon the remarkable Ranunculaceæ and Rosaceæ (*Anemone baldensis, Pulsatilla alpina, vernalis, Ranunculus alpestris, glacialis, Geum montanum, reptans*, &c.) which develop pseudo-hermaphrodite male flowers, as well as two kinds of hermaphrodite flowers, those with large ovary and few short stamens, and those with small ovary and numerous long stamens; but it may be stated that the former are adapted to crossing, and the latter to autogamy.

Another contrivance for promoting cross-fertilization is the interchange of position of anthers and stigmas. Although this has been repeatedly mentioned already (see pp. 250 and 276), it must again be described, since it represents one of the most important contrivances for the crossing of hermaphrodite flowers, and can only be completely understood when regarded from this point of view. The change of position consists essentially in this; the place occupied for some time by the ripe stigma is assumed later by the pollen-laden anthers, and *vice versâ*. Since this position is directly in the path traversed by the honey-sucking insect as it enters, the pollen is brushed on to the stigmas in one flower and collected from the anthers in another—a condition necessarily leading to cross-fertilization. This change of position is brought about by spontaneous movements in the anther-filaments, or by similar changes of direction in the styles. It may even happen that both the stamen-filaments and the styles of the same flower alter their position and actually exchange places. We may distinguish no less than *ten* different varieties of this change of position.

In one group of plants, of which the Dwarf Leek (*Allium Chœmœmoly*) may be taken as an example, the ripe stigma is seen in the middle of the newly-opened flower, while the anthers are pressed back against the perianth-leaves. Later, as the anthers open and expose their pollen, they pass towards the centre by reason of the peculiar movement of their filaments till they come close to the stigma and form a yellow ball. This is necessarily touched by an insect as it enters the

flower, although previously only the stigma would have been brushed in the same position.

In a second group, to which belong many Gentians (*Gentiana asclepiadea, ciliata, Pneumonanthe*), most Malvaceæ (*Abutilon, Malva*), the numerous species of Monkshood (*Aconitum*), *Funkia*, and the Red Valerian (*Centranthus*), the pollen in a young flower is exposed close to the path of the honey-seeking insect; sometimes only from a single anther (as in *Centranthus*, figs. 289 [1,2,3]), sometimes from five or six, or from quite a number united together in one bundle (Malvaceæ). The stigmas are at first hidden behind, *i.e.* below the anthers; later on the anther-filaments bend back in a semicircle, and the stigmas are exposed. When only a single stigma is present (hitherto hidden behind the anther as in *Centranthus*) of course only one can be displayed (see figs. 289 [2] and 289 [3]). When an insect comes for honey it strikes against the exposed stigmas, just as it did previously against the anthers.

The third group contains species of *Gladiolus, Acanthus*, Penstemon, and Sage (*Salvia*; see fig. 271, p. 262). The styles and stigmas of the horizontally-directed flowers of these plants lie close against the roof-like portion of the corolla above the anthers, but later the style bends down until the stigma lies just in the path which leads to the honey, so that insects passing this way (laden with pollen from the younger flowers) deposit it in older ones, so producing cross-fertilization.

In the fourth group, to which belong the genera *Allionia* and *Phalangium*, the stigma at the commencement of flowering is at the end of the projecting style in front of the anthers, and insects flying to the flowers are obliged to brush against this stigma. Afterwards the style bends sideways through an angle of 80–90°, so that the stigma is removed from the road leading to the honey. Now, when insects fly to the flower they come in contact with the pollen-covered anthers only.

In flowers of the fifth group, of which the Germander (*Teucrium*; see figs. 289 [4,5,6]) is a type, the change of position resembles that of *Centranthus* in that the thread-like anther-filaments are placed at the aperture of the flower, so that insects strike against the anthers as they enter. Afterwards the stamens bend up, and the anthers are removed from the path, whilst concurrently the stigmas are exposed. But there is this important difference—in the Germander the style as well as the stamens alters its direction and position and bends downwards like a bow till the stigmas come to lie in exactly the same position as was previously occupied by the anthers.

In the flowers of the sixth group, typical examples of which are furnished by the sweet Basil (*Ocymum Basilicum*) and the well-known climber, *Cobœa scandens*, the same kind of change of position occurs as in the Germander; but the stamen-filaments bend down instead of up, and the style upwards instead of downwards. At the beginning of flowering the anthers intercept the passage to the honey at the base of the flower, but later on they sink downwards, while the style arches up, bringing the stigma to the identical place previously occupied by the anthers.

The remarkable change of position of stigmas and anthers in plants of the

seventh group as shown by the Nightshade (*Atropa*), *Scopolia*, Henbane (*Hyoscyamus*) and the Mandrake (*Mandragora*) has been already described on p. 278 and illustrated in figs. 279[8] and 279[9]. In young blossoms the stigma stands in the middle of the flowers, and the anthers lie against the walls of the corolla: in older flowers the anthers stand in the middle, and the style becomes pressed against the corolla.

The shrubby species of Honeysuckle (*Lonicera alpigena, nigra*, and *Xylosteum*), and the genus *Scrophularia* may be taken as examples of the eighth group. Their flowers are horizontally placed. At first the straight style rises out of the centre of the flower, and the stigma is held directly in the path leading to the honey.

Fig. 280.—Change of Position of Anthers and Stigmas.

[1] Inflorescence of the Red Valerian (*Centranthus ruber*). [2] A single flower of the Red Valerian shortly after opening. [3] The same flower at a later stage. [4] Inflorescence of *Teucrium orientale*. [5] Single flower of the same plant shortly after opening. [6] The same flower at a later stage. [1] and [4] nat. size; [2], [3], [5], and [6] somewhat magnified.

The anthers are above the stigma in *Lonicera*, but in *Scrophularia* they are hidden at the end of their arched filaments in the cavity of the pitcher-shaped corolla. Later on the stigma is moved out of the path by the downward curvature or sharp bending of the style, the anthers assuming the position occupied by the stigma by means of a corresponding straightening and alteration of direction of their filaments.

The Hellebore (*Helleborus*), a type of the ninth group, has comparatively large flowers with abundant honey. The honey is not in the centre of the flower, as in the instances quoted above, but is secreted in cornet-shaped receptacles outside the ring of stamens. Accordingly the honey-sucking insects do not go to the centre of the flower but to the circumference, and this explains why the stigmas and anthers, which are to be brushed by the insects, are arranged in a corresponding circle. When the flower opens the styles radiate outwards, and are bent, so that the stigmas stand over the honey receptacles. The anthers are crowded together in the middle of the flower, and are not touched by the insect as it enters. Afterwards the styles straighten and move towards the centre of the flower while the stamen-filaments

elongate, and thus assume a position overhanging the honey receptacles, where they are inevitably brushed by insects.

For the tenth group we may select the Rue (*Ruta*; see fig. 290) as an example. The flower contains ten anthers supported by stiff filaments, arranged in the form of a star. First, one of these filaments bends up and places its anther in the middle of the flower, just in the way to the fleshy ring which secretes nectar at the base of the pistil: it remains there about a day, and then bends back and resumes its former position. While the first stamen is bending back, a second rises up and undergoes the same movements. And so it goes on until the ten anthers have all stood in the centre of the flower in turn and discharged their pollen there. When, finally, the last stamen has bent back again, the stigma, which has meanwhile matured, is seen in the centre of the flower where the anthers have successively shed their pollen.

Fig. 290.—Flower of the Rue (*Ruta graveolens*) × 3. (After Baillon.)

A process which is closely connected with the interchange of position of anthers and stigmas, in bringing about cross-fertilization between hermaphrodite flowers, is the separation and subsequent falling away of the stigmas when the surrounding anthers begin to dehisce. We may take one of the Urticaceæ, the Wall Pellitory (*Parietaria*; see figs. 291 [2, 3, 4]), as a type of this. The stigma is always developed before the flowers open in this plant, and at the commencement of the flowering period it may be seen projecting like a dusting-brush from the green flower-bud (fig. 291 [3]). The curved anther-filaments are at this time coiled like watch-springs and covered over by the as yet unopened floral-leaves. Before these filaments jerk up and scatter their pollen the stigma withers and shrivels up and the style becomes detached from the ovary. It falls off with the dried-up stigma, so that, when the pollen is liberated from the anthers, the ovary is terminated merely by a small stump which is really the withered remnant of the fallen style (fig. 291 [4]).

The falling of the anthers and stamens at the time when the adjoining stigmas become mature is of much more frequent occurrence than the detachment and falling of the stigmas before the pollen is shed. In the flowers of Balsams (*Impatiens glandulosa, Nolitangere, tricornis*, &c.) the anthers are united into a kind of cap which arches over the stigma. As soon as the flower has opened and become accessible to flying insects, the anthers dehisce and only the cap which they form can be seen at the entrance to the flower. Later, the filaments of the anthers become detached, and the anther-cap falls out of the flower; only the stigma, which has meanwhile matured, is now visible in the middle of the flower. The large-flowered species of Crane's-bill (e.g. *Geranium argenteum, pratense, sylvaticum*; see fig. 291 [1]) have a similar arrangement. Two of the anthers which have hitherto been covered by the petals dehisce almost simultaneously with the opening of the flower; the others then open in a certain order and expose their pollen in

turn. The stigmas in the centre of the flower are still folded together: as soon as they begin to separate the anthers fall away from their filaments, and the five mature outspread stigmas are surrounded only by the needle-shaped filaments minus their anthers (fig. 291 [1], the left-hand flower). The same thing happens in some Saxifrages, of which *Saxifraga rotundifolia* (fig. 292) will serve as a type. After the petals have unfolded, a peculiar action on the part of the stamens is to be observed for several days. Each anther as it dehisces is raised up by its filament into an erect position (see fig. 292 [2]), but remains in this position only for a short time; it bends down again the next day or the next but one, resuming its original position. The anther falls off, or if it remains as a shrivelled mass on the top of the filament it has by this time lost all its pollen. All the stamens in succession

Fig. 291.—Completely dichogamous Flowers.

[1] *Geranium sylvaticum* with completely protandrous flowers. [2] *Paristaria officinalis* with completely protogynous flowers. [3] Single flowers of *Paristaria* with mature brush-shaped stigma and closed coiled-up stamens. [4] The same flower at a later stage of development; the stigma has fallen off, the filaments have straightened, and the anthers are flirting out their dusty pollen. [1] and [2] nat. size; [3] and [4] somewhat magnified.

undergo this rising and sinking. Not until all the pollen has disappeared do the two short styles, which up till now have been folded together like the two ends of a pair of tongs (fig. 292 [2]), separate from one another, and their stigmas become capable of pollination (fig. 292 [3]). The Grass of Parnassus (*Parnassia palustris*; see fig. 267 [4], p. 249) as well as many Caryophyllaceæ (e.g. *Alsine verna*, *Silene Saxifraga*), many Valerians (e.g. *Valeriana officinalis*) and Tulips (e.g. *Tulipa Didieri*) exhibit the same course of development, especially the falling away of the anthers. In Caryophyllaceæ it often happens that the antherless filaments bend down in a semicircle under the petals and become so hidden that the flower might at first sight be thought to be pistillate instead of truly hermaphrodite.

The end gained by this shedding of the anthers in the Balsam, Saxifrage, Grass of Parnassus, Chickweed, Pink, and numerous other plants with hermaphrodite flowers, is also obtained in the following manner:—The anthers are covered over

and hidden by the petals as soon as the neighbouring stigma begins to mature, so that they are no longer able to shed their pollen. The consequence is that the stigmas can only be pollinated with foreign pollen, which is of course the same thing as saying that only cross-fertilization can occur in these hermaphrodite flowers. In the hermaphrodite flowers of the Spiderworts (*Tradescantia crassula, Virginica*, &c.), the anthers dehisce a considerable time before the stigmas mature. When the flower first opens, therefore, pollen only can be removed. But as soon as the stigmas become capable of fertilization the stamens roll up in a spiral, and soon afterwards the perianth withers and forms a moist, pulpy mass, quite covering the anthers on their rolled-up filaments. The style still projects stiffly from the flower and the stigmas remain capable of fertilization the whole of the following day. Small flies and other insects with short probosces now visit these flowers to suck up the juice of the pulpy petals, and at the same time the stigma is pollinated with

Fig. 292.—Dichogamy in *Saxifraga rotundifolia*.

[1] A portion of the inflorescence with flowers at different stages: that to the right still young, in the middle older. [2] Longitudinal section through a single flower with folded stigmas and one stamen shedding its pollen. Another stamen (to left of pistil) has lost its anther, and four others have anthers which have not yet dehisced. [3] The same flower at a later stage of development, with mature stigmas. [1] nat. size; [2] and [3] × 4–5.

pollen which they have brought from distant flowers, it being impossible to obtain that of the neighbouring anthers. It is an odd fact that some of the flowers of a *Tradescantia* plant, all of which opened simultaneously in the morning, will be already closed the same evening, whilst others will remain open the whole of the following day. It would seem that in those flowers which remain open the succulent hairs of the staminal filaments are devoured by flies, thus is the pollen obtained which is to be taken to the stigmas of the flowers whose anthers are hidden under the pulpy perianth. A peculiar process is observed in the flowers of *Telephium Imperati*, a native of Southern Europe, belonging to the Caryophyllaceæ. Here the anthers open first, but, as soon as the stigmas mature, the anthers—even if they have not as yet discharged all their pollen—are covered over by the petals, so that only pollen from other younger flowers can reach the ripe stigmas.

By these contrivances the same result is obtained in hermaphrodite flowers as by the separation of the two kinds of sexual organs on different plants, or on different flowers of the same plant. In all cases it seems to be the separation of the two kinds of sexual organs within the limits of the same species which is aimed at. The separation of the two kinds of sexual organs by the non-simultaneous maturation of the pollen and of the stigmas in any one species is just as effective in

promoting cross-fertilization as their separation by actual distance. In other words, separation in time is as efficient as separation in space; and these flowers, though structurally hermaphrodite (in that they contain both male and female organs), are —as the mechanism works out—unisexual (in that only one set of organs is mature at any given moment). This maturation of the sexual organs so that they are capable of fertilization at different times in the same plant, is termed *dichogamy*

Fig. 293.—Incompletely dichogamous Flowers.

[1] *Epilobium angustifolium* with protandrous flowers. [2] *Eremurus Caucasicus* with protogynous flowers.

(δίχα, apart, and γάμος, marriage), and we may distinguish between *protogynous* and *protandrous dichogamy*. If the stigmas are able to receive pollen, retain it, and stimulate it to put out pollen-tubes at a time when the pollen in the same flower is still unripe and hidden in the anthers, this particular species is termed *protogynous* (from πρῶτος, first, and γύνη, a woman). But if the pollen is shed from the dehisced anthers, whilst the stigmas in the same flower are yet immature, *i.e.* not susceptible to pollination, then the species is said to be *protandrous* (πρῶτος, first, and ἀνήρ, a man). In the racemose inflorescence of the Willow-herb (*Epilobium angustifolium*), which is represented in fig. 293[1], the upper flowers are seen to be still closed; a little lower are three flowers which have just opened, the middle one being visited by a

humble-bee, whilst lower still are flowers which have been open for two days. In the recently-opened flowers the anthers are covered with pollen, while the stigmas on the end of the downwardly-curved style are as yet immature and folded together into a club-like body. This plant is therefore protandrous. The inflorescence of *Eremurus Caucasicus*, belonging to the Liliaceæ, is figured beside it (293 [2]). Here, again, the youngest flowers are still in bud, those coming next below have just opened, whilst lower down still are the oldest flowers of all. In the newly-opened flowers the anthers are closed and no pollen is exposed, but the pointed stigma, terminating the upwardly-curved style, is already mature, so that this plant is protogynous. Both protandrous and protogynous dichogamy may be complete or incomplete. It is *complete* when the stigma begins to ripen after the removal of the pollen from the adjoining anthers by wind or by flower-visiting insects, so that it can no longer fertilize its own flower; or if the stigma is withered, dried up, or fallen away as soon as the anthers of the same flower open and expose the pollen or scatter it abroad, as in the Wall Pellitory (see figs. 291 [2, 3, 4]). Dichogamy is *incomplete* when the ripening of the two kinds of sexual organs is not, indeed, simultaneous, but when the capacity for fertilization of one sex is not at an end before the other sex in the same flower is mature. There are, of course, many grades in incomplete dichogamy. In long-lived flowers the start which one sex has over the other may amount to several days, but in short-lived flowers it may be limited to a few hours. Cruciferæ all have protogynous flowers. The already mature stigma is visible in the centre of the flower as soon as the petals open, but the surrounding anthers are still shut up. This only lasts for a short time; soon the anthers dehisce, and then both sexes come into operation. In *Lepidium Draba*, *Sisymbrium Sophia*, and numerous other species, this difference of time (lasting from the moment when the stigma is accessible to the moment when the anthers begin to shed the pollen) is only 2–5 hours. The same may be said of numerous Rock-roses, Papaveraceous plants, Cactuses, Ranunculaceæ, Rosaceæ, Boraginaceæ, Gentianaceæ, Ericaceæ, and Valerianaceæ (e.g. *Helianthemum alpestre*, *Glaucium luteum*, *Opuntia nana*, *Actæa spicata*, *Adonis vernalis*, *Atragene alpina*, *Clematis Vitalba*, *Potentilla caulescens*, *Cynoglossum pictum*, *Lithospermum arvense*, *Menyanthes trifoliata*, *Arctostaphylos uva-ursi*, *Vaccinium Myrtillus*, *Valerianella dentata*). Even the majority of ephemeral flowers exhibit dichogamy. The flowers of the Marvel of Peru (*Mirabilis Jalapa*) open between seven and eight o'clock in the evening; as soon as the margins of the flower unfold, the small stigma, resembling a tiny brush, is able to receive pollen, but the anthers are as yet entirely closed. About 10–15 minutes later the anthers dehisce and shed their pollen. The difference in the time is so slight here that it would be unnoticed by most people, and this explains why such flowers have not been regarded as dichogamous. But the very circumstance that the maturation of the two kinds of sexual organs is not simultaneous, even in ephemeral flowers, is of the greatest importance for the question of the significance of dichogamy and must be especially dwelt upon here.

In protogynous dichogamy it is no uncommon thing for the stigma to project from the flower already fitted to receive pollen whilst the petals are still closely shut, the whole flower having the appearance of a bud. This happens in the Curled Pondweed (*Potamogeton crispus*, figured on p. 148), in Asphodels (e.g. *Asphodelus albus*), in Woodrushes (e.g. *Luzula nivea*), in Elms (e.g. *Ulmus campestris*), in the Plantain (e.g. *Plantago media*), in several Rhododendrons (e.g. *Rhododendron Chamæcistus*), in *Cortusa*, *Deutzia*, and many other plants. On the other hand, many plants with protandrous dichogamous flowers are known where the pollen is shed from the anthers while the petals are still folded as in the bud. On opening the ripe bud of *Crucianella stylosa* (figured on p. 265), it can be seen at a glance that the anthers have already dehisced some little time, and have deposited their pollen under the dome of the closed bud on the thickened warty surface at the end of the style. In the flowers of *Rhododendron hirsutum*, the pollen falls from the anthers while still in the bud, and the same may be observed also in many Composites, Campanulaceæ, and Papilionaceous flowers.

We are not yet in a position to say whether protandrous or protogynous species are the more abundant, although the dichogamy of thousands of plants has been investigated. By generalizing on this subject one is liable to fall into very great error. It would be particularly dangerous to generalize prematurely on the results which have been obtained from the examination of many species of a genus, or many genera of a family, and to consider them to hold good for the whole group, for most genera contain some protandrous species, even when the majority of them are protogynous, and *vice versâ*. Liliaceous plants are described as protandrous in most Botanical books, but in reality many of the genera and species are incompletely protogynous (*Amaryllis*, *Asphodelus*, *Colchicum*, *Erythronium*, *Leucojum*, *Lilium Martagon*, *Narcissus poeticus*, *Ornithogalum umbellatum*, *Scilla*, *Trillium*, &c.). Among the Umbelliferæ, which are usually stated to be all protandrous, there are quite a number of protogynous genera and species, as, for example, *Æthusa*, *Astrantia*, *Caucalis*, *Eryngium*, *Hacquetia*, *Pachypleurum*, *Sanicula*, *Scandix*, and *Turgenia*. This also applies to the Saxifrages: the majority, of course, are protandrous, but some of them, viz. *Saxifraga androsacea* and *peltata* are decidedly protogynous. The large-flowered species of Crane's Bill (*Geranium argenteum*, *lividum*, *pratense*, *sylvaticum*) are protandrous, the small-flowered (*Geranium columbinum*, *lucidum*, *pusillum*, *Robertianum*) are protogynous. In the Scrophulariaceæ the genera *Digitalis* and *Penstemon* are protandrous, and the genera *Linaria*, *Pœderota*, *Phygelius*, *Scrophularia*, *Veronica* protogynous. Of species belonging to Boraginaceæ some are protandrous (e.g. *Borago*, *Echium*), others protogynous (e.g. *Cynoglossum*, *Lithospermum*). In Ranunculaceæ the genus *Aconitum* is protandrous, while the genera *Adonis*, *Anemone*, *Atragene*, *Clematis*, and *Pæonia* are protogynous. In the Gentian family some are protandrous, viz. *Swertia perennis*, *Gentiana asclepiadea*, *ciliata*, *cruciata*, *Frœlichii*, *Pannonica*, *Pneumonanthe*, *punctata*, and *prostrata*; others, especially *Menyanthes trifoliata*, *Gentiana Bavarica*, *Germanica*, *glacialis*, *Rhætica*, and *verna* are

protogynous. The same is true of Ericaceæ, Valerianaceæ, Polemoniaceæ, and many other groups. As far as we know, the Composites, Campanulaceæ, Labiatæ, Malvaceæ, Caryophyllaceæ, and Papilionaceous plants are exclusively protandrous, Rushes and Woodrushes (*Juncus* and *Luzula*), Aristolochiaceæ and Thymelaceæ, Caprifoliaceæ, Globularias, Solanaceæ, Rosaceæ, Berberidaceæ, and Cruciferæ exclusively protogynous.

It has already been pointed out that the non-simultaneous maturation of the sexual organs goes hand in hand with the separation in space of the two sexes in most instances, or, in other words, that in plants where the two kinds of sexual organs have in any way been separated from one another in the flowers by actual distance, dichogamy also obtains. Thus, for example, it appears that all species of plants whose hermaphrodite flowers are adapted to cross-fertilization by the relative position and arrangement of their two kinds of sexual organs, or by the interchange of position of anthers and stigmas are, moreover, dichogamous, although this dichogamy may be only of slight duration. Plants with heterostyled flowers are also dichogamous, since those with short-styled and those with long-styled flowers develop at different times. If one observes the many hundred individuals of *Primula Auricula*, growing side by side on a rocky crag under the same conditions, it is easy to see that the plants with long-styled flowers are earlier than those with short styles. The former are already over while the latter are in full bloom. The reverse is the case in *Auricula longiflora*; here plants with short-styled flowers are in full blossom when the long-styled flowers of the neighbouring plants are still in bud.

Plants bearing pseudo-hermaphrodite flowers are also dichogamous. The Valerians (*Valeriana dioica, polygama*, and *tripteris*) open their pistillate flowers 3–5 days before their staminate flowers in the same locality; these plants are therefore decidedly protogynous. In the Alpine Dock (*Rumex alpinus*), the stigmas of the pistillate flowers are ripe 2–3 days before the anthers of the staminate flowers and of the truly hermaphrodite flowers on the same plant have opened. In the Ash (*Fraxinus excelsior*), the stigmas of the pistillate flowers are mature whilst the anthers in the neighbouring staminate and hermaphrodite flowers are still closed. The latter do not usually shed their pollen till 4 days later. The dichogamy of the Grasses, which bear both true staminate and hermaphrodite flowers, is very striking (e.g. *Anthoxanthum odoratum, Hierochloa australis, Melica altissima*, and *Sesleria cœrulea*). In these plants the anthers do not liberate their pollen until the neighbouring stigmas have been mature for two days. This may also be observed in Composites whose capitula contain true hermaphrodite and pistillate flowers, and in those with true pistillate and pseudo-hermaphrodite male flowers. The stigmas of the pistillate flowers are already mature two days before any pollen can be obtained from the adjoining truly hermaphrodite or staminate flowers. It will suffice to mention as examples of this *Aster alpinus, Aronicum glaciale, Bellidiastrum Michelii, Doronicum cordatum, Erigeron alpinum, Gnaphalium Leontopodium, Tussilago Farfara*, and *Calendula offici-*

nalis. Labiates which bear only true hermaphrodite flowers on one plant, and only pseudo-hermaphrodite female flowers on another are protogynous. In the Marjoram (*Origanum vulgare*), the pistillate (pseudo-hermaphrodite female) flowers are ripe as much as eight days or longer before the true hermaphrodite flowers. The fact must be emphasized that these remarks only refer to such flowers or plants as develop under similar conditions of life, and that they are not applicable to instances where the early or late maturity depends upon whether the habitat is a sunny or shaded one.

As far as we can tell at present all monœcious plants are protogynous. Sedges, Bulrushes, Bur-Reeds (*Carex, Typha, Sparganium*), Aroids with monœcious flowers, the Maize (*Zea Mays*), the monœcious Stinging Nettle (*Urtica urens*), the Water Milfoil (*Myriophyllum*), the Burnet (*Poterium*), the Burweed (*Xanthium*), the monœcious Euphorbiaceæ (*Euphorbia, Ricinus, Buxus*), and especially Alders and Birches, Walnuts and Planes, Elms and Oaks, Hazels and Beeches, are all markedly protogynous. In most of these plants, especially the last-named trees and shrubs, the dust-like pollen is not shed from the anthers until the stigmas on the same plant have been matured 2–3 days. Sometimes the interval between the ripening of the sexes is still greater. The majority of dicœcious plants also are protogynous. In the luxuriant Willows on the banks of rivers a single species is sometimes represented by thousands of bushes. Some of them bear staminate, the others pistillate flowers. They grow on the same soil, are exposed to the same amount of sunlight, and are fanned by the same breezes, and yet, in spite of identical external conditions, the plants with pistillate flowers certainly precede their staminate neighbours. The stigmas of the Almond Willow (*Salix amygdalina*) are already mature 2–3 days before a single anther of this species has dehisced anywhere. The same happens in the Purple-willow, Osier, and Crack-willow. This phenomenon can also be observed in the sub-alpine Willows (*Salix herbacea, retusa, reticulata*), but here the difference in time is usually restricted to a single day. Among the countless plants of Hemp (*Cannabis sativa*), which grow up together in the summer in closest proximity from seeds sown on level fields, most of the individuals which bear pistillate flowers have already protruded their stigmas before a single staminate flower has opened. The latter do not unfold until 4–5 days after the pistillate plants have begun to blossom, and then only does the wind scatter the pollen from their versatile anthers. In the Dog's Mercury, especially in the perennial species of the genus (*Mercurialis ovata* and *perennis*) which grow in small clumps in the depths of our woods, plants with pistillate and others with staminate flowers being close together on the same soil, the stigmas are capable of fertilization at least two days before the pollen is shed. The same thing is observed in the Hop (*Humulus Lupulus*), and in many other dicœcious plants.

All these facts are of the greatest importance in the question of the significance of cross-fertilization. If the maturation of the sexes at different times had been observed only in those species of plants which bear hermaphrodite flowers, dichogamy might be regarded merely as the completion of the contrivances for preventing

the pollen from fertilizing the stigmas of the same flower, *i.e.* for preventing self-fertilization or autogamy. For example, the relative position of the anthers and stigmas in the flowers of the Arrow-grass (*Triglochin*; see fig. 237, p. 149) renders it almost impossible for the pollen to reach the stigmas in the same flower, but the possibility would not be excluded were the anthers to shed their pollen at the time when the stigmas were capable of being fertilized. Since, however, in the flowers of the Arrow-grass, the stigmas are quite dried up at the the time of dehiscence, autogamy is quite impossible, and so far dichogamy is a completion of the contrivances mentioned. But such cases of complete dichogamy as in the Arrow-grass, the Wall Pellitory, and the Grass of Parnassus, &c., are comparatively rare, and this explanation will not hold for the great bulk of hermaphrodite flowers which are incompletely dichogamous. Still less will it apply to monœcious and dicecious plants. Here there is no question of autogamy or self-fertilization, and for this reason all hypotheses founded on the prevention of self-fertilization by dichogamy are futile.

We cannot suppose, however, since the non-simultaneous maturation of the sexes is a phenomenon which occurs in most—perhaps in all—plants, that this contrivance has no meaning. I will now endeavour to elucidate the significance of dichogamy and invite the reader, first of all, to enter one of the Willow plantations which have been briefly described above. The Purple Willow (*Salix purpurea*) is just beginning to bloom. The pistillate flowers already display mature stigmas; but the staminate flowers are still behind, and not a single anther has opened. The staminate flowers of the Osier (*Salix viminalis*), on the other hand, growing in the same clump with the Purple Willow, are in their prime. The pollen of the Osier is to be had in any abundance. Numerous bees have been attracted by the scent and colour of the male catkins, and they buzz from bush to bush, sucking the honey and collecting pollen. They are not dainty in their work, and do not limit themselves to one species but fly impartially to the Purple Willow, to the Osier, or to other species of Willow which may happen to be present. Now, if a bee comes to suck the honey from the pistillate flowers of the Purple Willow, after it has just visited another Willow bush, where it has covered itself with pollen, obviously that bush must have been the Osier, Sweet Willow, Sallow Willow, or some other species, whose staminate flowers have already developed so far as to render their pollen accessible. It cannot have been a Purple Willow, because not a single anther of this species in the whole neighbourhood has yet opened. But since the stigmas of the Purple Willow are thus fertilized by the pollen of the Osier, &c., hybridization occurs. Two or three days later, a legitimate crossing may take place, for, by this time the anthers of the Purple Willow will have protruded from the staminate flowers and opened widely, and abundance of pollen will be afforded to insects. These are not slow to visit the now accessible flowers, and they remove some of the pollen and transfer it to the stigmas of the same species which are still capable of being fertilized. Thus at the commencement of flowering hybridization is alone possible, and legitimate cross-fertilization cannot take place till some time later,

in consequence of the dichogamy of these Willows. This obviously applies to all other Willows, and generally to all dicœcious plants whose flowers are incompletely protogynous.

In order to show that the same processes obtain in moncœcious plants, I would ask the reader to accompany me to the edge of a moor where numerous moncœcious Sedges (*Carex*) form the chief constituents of the vegetation. Widely different species grow in varied profusion side by side. Here at the margin of a dark pool *Carex acutiformis, filiformis, riparia, vesicaria, paniculata*, there, on the marshy stretch close by, *Carex flava, canescens, glauca, Hornschuchiana*, and many others. These Sedges do not all blossom at the same time; one ceases to flower just when another is in its prime, and when, in a third sort, the flowers have just begun to fade. All moncœcious Sedges are protogynous. The stigmas have been ripe 2–3 days, and have protruded far beyond their subtending bracts, so that it would seem natural that the pollen, wafted by the wind, would remain attached to them. But the anthers of the staminate flowers of the same species have not yet opened. It is evident then that the stigmas must be pollinated during the first and second day with pollen from other species which blossom earlier, for since the anthers of these earlier species are already open, each gust of wind will shake out their pollen and blow it over the moor, pollinating everything which is capable of being pollinated. The pollen of the same plants (afterwards shed from the staminate flowers above and close to the mature stigmas) can only be received in the second place on account of its later arrival. Thus, we see that incomplete dichogamy promotes hybridization in the first place, and then, only later, a legitimate cross-fertilization in plants with moncœcious flowers.

It is well known that all the plants of a species growing under similar external conditions do not blossom on the same day, and this fact is worth noticing in so far as it might be thought possible for the earlier plants of a species to provide pollen for the stigmas of later plants. This is certainly often the case, but it is also certain that the stigmas of the very earliest plant of a protogynous species can only be, and actually are, fertilized with pollen from another species which flowers still earlier; thus the conclusion already arrived at must remain unaltered.

It may be taken for granted, since plants with pseudo-hermaphrodite flowers behave exactly like dicœcious and moncœcious flowers in the manner of the transfer of their pollen, that their dichogamy has the same significance. The spikes of Docks belonging to the group *Lapathum*, viz. *Rumex alpinus, nemorosus*, and *obtusifolius*, bear principally pseudo-hermaphrodite flowers, which are some of them male, some female, and besides these a few true hermaphrodite flowers. In any one plant, the development of the stigmas is always considerably in advance of that of the anthers. The stigmas are ripe whilst the anthers are still closed. Under these circumstances the first flowers of a plant, whether pseudo- or truly hermaphrodite, can only receive pollen from other plants which have been in bloom for several days, and whose dehisced versatile anthers have been robbed of their pollen by the wind. It may further be taken for granted that any hundred plants of *Rumex obtusifolius*,

growing together in a clump, will not all blossom together, and consequently innumerable crossings take place between the flowers of the individuals of this same species. The first ripe stigmas of the earliest plants of *Rumex obtusifolius* within an hour's walk can only receive their pollen during the first two days from other species of Dock, and therefore, when they first blossom, hybridization only can occur. It has already been stated that plants of Marjoram (*Origanum vulgare*, a Labiate), which bear pseudo-hermaphrodite female flowers, blossom fully eight days before those with truly hermaphrodite flowers. To this we might add that the plants which blossom first in any given district cannot obtain pollen from the same species, and that consequently, if the stigmas are, nevertheless, pollinated by insects, the pollen must have been obtained from some other species. In Compositæ, whose capitula contain both truly hermaphrodite and pseudo-hermaphrodite female flowers, the latter always mature some days before the former, and consequently the pioneer flowers in a given locality can only obtain pollen from species which bloom still earlier, so that again hybridization occurs. In the floral region of the Black Sea many Fleabanes grow side by side (*Inula Oculus-Christi, ensifolia, Germanica, salicina*, &c.), and in the summer they blossom in definite succession, so that one species always begins to fade when another is in its prime. Each capitulum of these Inulas consists of tongue-shaped pseudo-hermaphrodite female flowers on the circumference and tubular hermaphrodite flowers in the centre. The former unfold earlier than the latter, and for each species there is a certain period, if only two days, when the pollen, brought by insects to the stigmas of the pistillate flowers on the circumference, can only have been obtained from another species, since their own pollen is not obtainable. Many other examples of the same kind might be quoted, all pointing to the fact that hybridization at the commencement of flowering and the subsequent legitimate crossing depend mainly on the incomplete dichogamy obtaining in these plants.

It is the same with plants which have true hermaphrodite flowers. In heterostyled species either the long-styled or the short-styled flowers may develop first. The long-styled flowers of *Primula Auricula* and the short-styled flowers of *Primula longiflora* are the earlier, consequently, the stigmas of the first long-styled *Primula* plants can only be fertilized with pollen from other species. This is often actually effected by insect-agency, and gives rise to numerous *Primula* hybrids. The same thing is repeated in hermaphrodite flowers which are not heterostyled. When a plant is protogynous, as, for example, the open-flowered Pasque-flower, *Pulsatilla patens*, the earliest flowers can receive no pollen from anthers of their own species, because not one is open, but it would be possible for them to be provided with the pollen of other species of the same genus which inhabit the same locality but blossom earlier. This, of course, only holds good for the *commencement* of the flowering period, and only for those plants of the species which are the first to open their flowers in a given place. At a later period of flowering legitimate crossing will occur, because by that time the earliest plants have shed their pollen, and it may be collected and transferred by insects. Among hermaphrodite plants

there are many whose flowers are not protogynous but protandrous. Here the stigmas of the earliest flowers of a species cannot be pollinated, because they are immature and inaccessible. What, then, becomes of the pollen of these first protandrous flowers? If it is carried by the wind or by insects, as soon as it is liberated from the anthers, to any stigma, that stigma must of necessity belong to another species which has already become receptive. Towards the end of the flowering period, the pollen usually runs short in most protandrous species, whilst the stigmas of these stragglers have only just attained maturity. They could only obtain pollen from flowers which had not developed so far. But if these flowers are the last in the locality, and they are protandrous, there is no more pollen to be had from that species, and obviously they must be satisfied with pollen from some other. Accordingly hybridization is a matter of necessity in the latest flowers of hermaphrodite plants which are protandrous, just as it is in the earliest flowers of those which are protogynous.

From these facts we may infer that every dichogamous plant has an opportunity for illegitimate crossing or hybridization at the beginning or end of its flowering, and that dichogamy—especially incomplete dichogamy—is the most important factor in its production. Of course this does not exclude dichogamy from playing an important part in legitimate crossing as well. On the whole, however, we can maintain the view that the separation of the sexes by the maturation of the sexual organs at different times leads to hybridization, whilst their separation in space promotes legitimate crossing. The fact that the separation of the sexes in time and space usually occur in conjunction, harmonizes with this conclusion, *i.e.* that the dicœcious, moncœcious, and pseudo-hermaphrodite flowers, as well as those hermaphrodite flowers whose sexual organs are separated by some little distance, are in addition incompletely dichogamous, because by this contrivance the flowers of any species obtain (1) the possibility of hybridization at the beginning or end of their flowering period, and (2) of legitimate crossing during the rest of that time. This also explains why incomplete dichogamy is so much more frequent than complete dichogamy; why there are no dicœcious species of plants with completely dichogamous flowers; and why, if one ever should occur, it would of necessity soon disappear. Let us suppose that somewhere or other there grows a species of Willow with completely protogynous dicœcious flowers, that is to say, a species in which the female flowers mature first, and have ceased to be receptive before the male flowers in the same region discharge their pollen. Hybridization only could occur in it, and the young Willow plants resulting from it would all be hybrids whose form would no longer agree absolutely with that of the pistilliferous plant. The species would therefore not be able to reproduce its own kind by its seed, and it would leave no descendants of similar form; in other words, it would die out.

Two varieties of legitimate crossing, caused by the separation of the sexes by actual distance, have already been mentioned (see p. 301), viz., *Xenogamy* and *Geitonogamy*. We speak of xenogamy (from ξένος, a stranger, and γάμος, marriage) when the flowers in question belong to different individuals of the same species,

and of geitonogamy (from γείτων, a neighbour, and γάμος, marriage) when the two flowers are on the same plant. We cannot, however, draw a sharp line between the two. The offshoots of a plant, which become ultimately isolated, forming independent plants, are, in point of origin, identical with the branches of a plant which remain attached. Accordingly, when a crossing occurs between flowers produced on plants that have arisen from one another by offshoots, the process is not essentially different from the crossing which takes place between flowers on adjacent branches. It is nevertheless convenient to keep the two cases distinct, on account of certain processes connected with the greater or lesser distances between the flowers.

Both in xenogamy and geitonogamy the transport of the pollen is effected partly by wind and partly by flower-visiting insects. How this is carried out, and the endless variety which exists, has been dealt with in detail in previous chapters. Geitonogamy is not infrequently, however, brought about in other ways, as by the pressing of mature stigmas on the liberated pollen of neighbouring flowers, or by the actual falling of pollen upon them. Since these methods of cross-pollination have only been incidentally touched upon, they must be described here somewhat more fully.

The conditions for crossing between neighbouring flowers are simple when the flowers are crowded in heads, umbels, bunches, spikes, and the like, standing so close together that the stigmas of one flower can easily touch the pollen-covered anthers of another. And since this kind of crossing is actually very widespread and is repeated in certain species with great regularity, generation after generation, we are justified in regarding these forms of inflorescence as being particularly associated with geitonogamy, and in assuming that a not unimportant advantage of a crowded inflorescence lies in the possibility of crossing between the neighbouring flowers of a plant (see vol. i. p 740).

As we might expect, this particular form of crossing occurs with great frequency in Compositæ, whose flowers are crowded so densely into capitula that the whole inflorescence might be taken, at first sight, for a single flower; consequently this extensive family of plants, which includes more than 10,000 species, will be the most suitable in which to describe the phenomenon of geitonogamy. We will commence with those Composites whose heads only contain "ray" or ligulate florets. The term ray or ligulate floret is applied to florets whose corolla is tubular only at the base, the free end being flattened and projecting outwards like a tongue or strap, as in the Dandelion. In *Prenanthes* each capitulum consists of only five such ray-florets. In each floret the long, thin style is inclosed in a tube of anthers. The style is covered with stiff outwardly-directed bristles which are called "sweeping hairs". When the style elongates, immediately after the opening of the flower, these hairs sweep out the pollen which has been already shed into the interior of the anther-tube. The long style, rendered quite yellow by the pollen it carries, now projects from the empty tube of anthers. The two branches of the style which bear the stigmatic surface are at first folded together, but they soon separate, and the stigmas can then be fertilized by the aid of insects with pollen brought from

other plants, but not with that which lies on the sweeping hairs below the stigmas. As soon as the strap-shaped corollas begin to wither and shrivel, the two stylar branches diverge strongly, and twist and turn like tiny snakes sideways and downwards. At the same time adjacent styles come nearer to one another, and it is therefore natural that the stylar branches of neighbouring flowers should get entangled. In this way the stigmas of one flower (which are still in a receptive state) necessarily come in contact with the pollen on the sweeping hairs of another, and pollination ensues.

The same process occurs in the flowers of the Lettuce (*Lactuca*), the Alpine Sow-thistle (*Mulgedium*), and in *Chondrilla*, only here the heads contain more florets than in the form just described. The stylar branches do not undergo snake-like movements, but they diverge widely and roll back a little, an action altogether sufficient to bring them into contact with the styles of neighbouring flowers and to promote a crossing. It is worth noticing that the corollas of the ray-florets of *Prenanthes* roll outwards when they begin to fade, while those of the Lettuce and of the other Composites mentioned fold up and form a hood over the stylar branches during crossing. The Salsify (*Tragopogon*), Hawkweed (*Hieracium*), *Crepis*, *Scorzonera*, Hawkbit (*Leontodon*), Dandelion (*Taraxacum*), and many other Composites, of which these plants may be regarded as typical, contain in each head as many as 100 ray-florets arranged in spiral series (*cf.* fig. 222[5], p. 112). The strap-shaped corollas separate in the morning and fold together in the evening, and similarly the anther-tubes and styles are inclined somewhat to the circumference of the capitulum in the morning, but come close together and assume an upright position in the evening. This gradual approach ultimately becomes actual contact, and since the development of the protandrous florets proceeds from the circumference towards the centre of the capitulum, the stigmas of the outer florets are mature at the time when the pollen has only just been swept out of the anther-tubes of the inner florets. The contact of the adjoining flowers, therefore, necessarily leads to cross-pollination. The fact that the corollas of the ray-florets in any capitulum are of unequal length (fig. 222[5], p. 112) has also a close bearing on this process. If they were all equally long this contact and crossing would be impossible, for division walls would be interposed between the styles of the outer and inner florets. But the inner corollas are just short enough to allow the styles to touch one another. In many of these plants, *e.g.* in the Salsify (*Tragopogon*), geitonogamy is also assisted by the arrangement of the flowers in each capitulum, each flower of an outer row being placed exactly between two of the next inner series. When the capitulum closes, the two curved stylar branches of an outer floret, with their exposed stigmatic surfaces, become applied to the pollen-covered styles of the inner flowers immediately to right and left in front of them.

There are comparatively few species of Composites having exclusively tubular florets in which cross-pollination occurs between the members of the same capitulum. The most remarkable of these species belong to the Hemp Agrimony genus (e.g. *Eupatorium aromaticum* and *cannabinum*; see figs. 294[1] and 294[2]). The capitula

contain but few florets; those of *Eupatorium cannabinum* have five, which open one after another in the course of 5–8 days. Younger and older flowers are therefore always close together. The styles are rather different from those of other Composites, being divided almost half-way down into two long threadlike branches which bear the stigmatic tissue only on their lower portions. The rest of the branch is thickly studded with short bristles, the aforesaid sweeping hairs. The styles are parallel and folded together as long as they are inclosed in the anther-tube (see fig. 294[2]), and they remain closed for some time after they have elongated and

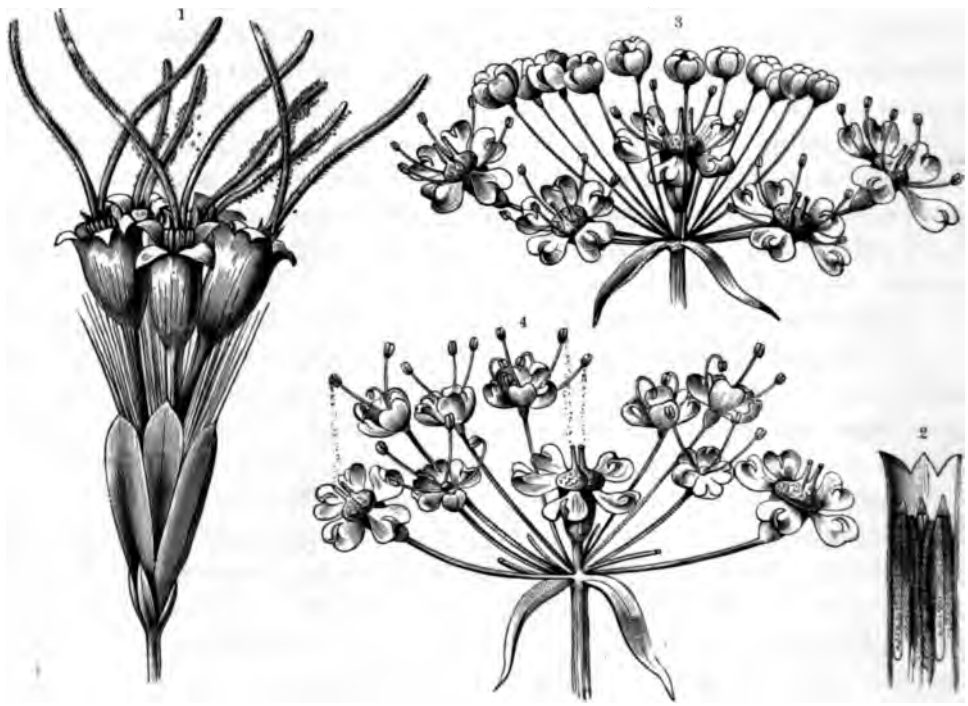

Fig. 294.—Geitonogamy with adherent pollen.

[1] Crossing of the stylar branches of neighbouring florets in the capitulum of *Eupatorium cannabinum*. [2] Longitudinal section through the upper part of a floret of *Eupatorium*; the two stylar branches are parallel and inclosed by the anther-tube, which is again surrounded by the corolla-tube. [3] Umbel of *Chærophyllum aromaticum*; the truly hermaphrodite flowers are open, the pseudo-hermaphrodite male flowers are still closed. [4] The same umbel; the true hermaphrodite flowers have lost their pollen; the male flowers are now open, and their anthers drop pollen on the stigmas of the hermaphrodite flowers. All the figures somewhat enlarged.

pushed their way above the anthers. During the elongation the sweeping hairs brush the pollen from the anther-tube, and it then adheres in abundance to the outer side of each style-branch. This condition, however, does not continue for long. The stylar branches soon diverge at an angle of 40–50°. The branches of adjacent styles now cross one another like rapiers, and when the pollen is detached from the sweeping hairs it falls on to the mature stigmatic tissue. The closed pollen-covered stylar branches, as they emerge from the anther-tube, come in contact with the divergent branches of older neighbouring florets, and thus the pollen is transferred to the stigmatic tissue of the latter.

The capitula of the Colt's-foot (*Tussilago*) and of the Marigold (*Calendula*) contain two kinds of florets. In the centre are pseudo-hermaphrodite male flowers, whilst true pistillate ray-florets form the fringe of the capitulum. The latter open earlier than the disc-florets, and therefore at first can only be fertilized with pollen from other capitula which are further advanced. But soon the pollen is pushed out of the disc-florets of the same capitulum, and is deposited in a small clump at the top of the anther-tube. This pollen is conducted to the stigmas of the neighbouring ray-florets by different methods in the two genera mentioned. In the Colt's-foot the numerous ray-florets at the periphery are expanded horizontally during the daytime, but towards evening they fold up, and in this way, as they bend over the tubular florets, contact with their clumps of pollen is unavoidable. The pollen is transferred to the ray-florets, and when the capitula open again next morning, and the ray-florets bend outwards, the adherent pollen is freed, and slips down to the ripe stigmas at the base of the corolla. The process is far simpler in the Marigold. The stylar branches of the ray-florets are bent inwards over the adjoining disc-florets while the latter are still closed. When they open, and the pollen is swept out of their anther-tubes, it of course passes inevitably to the stigmas of the neighbouring ray-florets which are situated just above.

The Golden-rod (*Solidago*), Aster (*Aster*), and many other Composites classed together in the group of the Asteroideæ, closely resemble the Colt's-foot and Marigold in outward appearance, but their sexes are differently arranged. The tubular disc-florets are all truly hermaphrodite, and the outer ray-florets are truly pistillate. The latter mature first, and are adapted to hybridization, as we have already remarked. Two days later the hermaphrodite flowers of the disc open—those towards the circumference being the first. Their pollen is pushed out, and meanwhile the flowers bend slightly outwards, so that the pollen lying on the anther-tubes in the form of small clumps either comes into direct contact with the ripe stigmas of the marginal ray-florets or falls on to them from a short distance.

In very many Composites the capitulum contains only hermaphrodite flowers with tubular corollas. The development of the flowers again proceeds from the circumference towards the centre of the capitulum, and in each flower, soon after the corolla has opened, the pollen is swept and pushed out of the anther-tube by the sweeping hairs or warts on the outer side of the style. The pollen forms a small clump at the mouth of the anther-tube, but does not retain this position long. The two stylar branches which have hitherto been folded together (their outer surface being coated with pollen) soon separate and often bend back in a curve so as to expose their ripe stigmatic surfaces. The pollen is thus for the most part detached in small crumbling balls which simply tumble down. In this way they reach the ripe stigmatic tissue of the older neighbouring flowers and geitonogamy ensues. Various contrivances are met with in these Composites to prevent the pollen which falls from the younger flowers from missing its mark, and to ensure its arrival on the stigmas of the nearest older flowers. In *Homogyne alpina* (an alpine plant related to the Butterbur) the tubular florets on the flat receptacle of the

capitulum are of unequal length. The marginal florets are rather shorter than the central ones, so that the stylar branches of the former are lower than those of the latter. But this is not enough to bring the pollen which has fallen from the higher stylar branches on to the stigmatic tissue of these older lower ones—since the lower are situated rather nearer the circumference of the capitulum, and it is therefore necessary that the pollen-bearing styles should incline outwards if their pollen is to reach its proper destination. This is what actually happens. The originally straight and erect styles bend outwards at an angle of 70–90°, even before their branches have separated, and while they yet retain the pollen which they have collected from the anther-tubes. When it is thrown off, it thus unavoidably reaches the lower stigmas of the older flowers. Or sometimes it happens that the divergent stylar branches of the younger flowers with attached pollen come into direct contact with the stylar branches of older flowers, and that geitonogamy is effected in this way.

Numerous other Composites whose capitula are composed entirely of tubular hermaphrodite flowers exhibit the same processes as *Homogyne*, which has been chosen here as a type. The Wormwoods of mountain heights, e.g. *Artemisia Mutellina* and *spicata*, exhibit a slight deviation. In them the central florets are raised above the marginal ones, not only by their greater length, but because the receptacle on which they stand is considerably arched. Obviously the florets at the top of the dome will stand higher than those round its circumference. In very many Composites (*e.g.* in *Doronicum glaciale* and *scorpioides*, in *Senecio cordatus*, in *Telekia*, *Buphthalmum*, *Anthemis*, and *Matricaria*), the receptacle is at first flat or but slightly arched; but during the flowering period it rises up so much that it assumes the form of a hemisphere, or even of a cone. This elevation in *Doronicum*-capitula, for example, amounts to 1 cm., and it is relatively even more in species of *Anthemis* and *Matricaria*. The immediate consequence of this change in the receptacle is of course an alteration in the direction of the flowers which stand on it. Flowers which stood erect on the receptacle of the capitulum when it first opened, assume later an almost horizontal position. But the most remarkable thing is that these changes keep pace with the advancing development of the flowers. In capitulate inflorescences the marginal flowers open first, and those in the centre last (see vol. i. p. 740). The flowers of each outer series are therefore always further advanced than those of the adjoining inner series, and when the mature stigmas are already opened in the outer flowers, the pollen of the inner ones is only just being pushed out of the anther-tubes and shaken off the stylar branches as they separate. A wonderful contrivance now meets our gaze—the mature stigmas of the outer flowers are brought directly under the inner flowers so as to catch their pollen as it falls, a condition brought about by the alteration in form of the receptacle on which all the flowers stand. Sometimes the pollen does not need to fall, for the flowers stand so closely side by side and above one another that the divergent stigmas of the older flowers come at once into direct contact with the pollen of the younger flowers. This is the case in various species of the Groundsel genus (*Senecio*) where the two stylar

branches diverge, not in a horizontal but in a vertical plane, the consequence being that one of the stylar branches comes in contact with the clumps of pollen just pushed out from a neighbouring higher flower. Of course there exist among Compositæ flowers quite a number of forms intermediate between those here described, all of which promote geitonogamy, but we cannot enter upon them further.

Among Umbelliferous plants, as in Compositæ, the numerous small flowers are crowded so closely together that the stigmas and pollen of neighbouring flowers can easily touch and combine, and a glance at these inflorescences is enough to suggest the possibility of geitonogamy. The conjecture is confirmed on a closer scrutiny, for the Umbelliferæ, as a matter of fact, exhibit an even greater variety of contrivances for geitonogamy than do the Compositæ. The most important of these will now be detailed. First, let us examine the group which is typified by the genera *Eryngium* and *Hacquetia*. In these the flowers are crowded together in capitulate masses surrounded by broad conspicuous bracts. They are all hermaphrodite and protogynous. The stamens with closed anthers are bent inwards in each flower like hooks, and the petals are still unfolded, but the sticky, shining stigma on the top of its long style already projects some distance out of the bud. At this stage the stigma can only be pollinated with pollen from other plants, indeed, from other species. Later, the stamen-filaments elongate and straighten, whilst the anthers dehisce, and pollen appears through the clefts. This pollen comes into contact either at once or very soon with the still receptive stigmas; for the long styles have meanwhile inclined more to the side, so that their stigmas are placed in such a position with regard to neighbouring flowers that either they brush against the pollen-covered anthers, or else are pollinated with the crumbling pollen which falls from these anthers.

The genera *Sanicula*, *Astrantia*, and *Laserpitium*, differ somewhat from this group of Umbelliferæ. The chief modification is that in the species of these three genera staminate as well as hermaphrodite flowers occur. In *Sanicula* each umbel consists of 3 true hermaphrodite flowers in the centre, and 8–10 staminate flowers arranged round them like a wreath. The hermaphrodite flowers are protogynous and the first to develop, so that at the beginning of flowering the stigmas can only be fertilized with the pollen from plants of other species. The stamens straighten afterwards and project like the style far out of the flowers. But the anthers and stigmas of the same flowers do not touch, since the styles stand up erect, whilst the stamens have an oblique direction. A crossing soon takes place, however, between the hermaphrodite flowers and the adjoining staminate flowers, in the following way. The stamens of the hermaphrodite flowers wither and fall off, and the stigmas of these flowers become divergent, curving slightly outwards, so that their still receptive surfaces are brought into the surrounding circle of stamens. The anthers of the male flowers have meanwhile dehisced and are shedding abundant pollen. The stigmas are necessarily pollinated either by the direct contact of stigmas and anthers, or, by the falling of the pollen from these anthers. The arrangement of the flowers in *Astrantia* has already been described on p. 296; it

agrees with *Sanicula* in having hermaphrodite and staminate flowers in each umbel, the hermaphrodite flowers developing first and being protogynous, so that again the sticky stigmas of the first-opened flowers in a given locality can only be fertilized by the pollen of other species. Later, the stigmas of the hermaphrodite flowers separate, and to a certain extent offer themselves to the pollen of the neighbouring staminate flowers which is now being shed. *Laserpitium* exhibits the same general arrangement of flowers as *Sanicula* and *Astrantia*, but the hermaphrodite flowers in the large, loose umbel are protandrous instead of protogynous. Geitonogamy, however, obtains, just as in *Astrantia*, by the stigmas at the top of the divided style exposing themselves to the pollen from the anthers of the neighbouring staminate flowers. Since the protandrous hermaphrodite flowers open before the staminate ones, their stigmas are mature exactly at the same time that the anthers of the latter shed their pollen.

A notable exception to these Umbelliferæ which have been described, where the stigmas of one flower obtain the pollen from neighbouring flowers by the elongation and bending of their styles into their neighbour's domain, thus producing geitonogamy, is afforded by others whose styles and stigmas retain their original position. The stamens, however, elongate and straighten, and assume such a position that the pollen liberated from their anthers can reach the stigmas of the neighbouring flowers. One group of such species, of which *Pachypleurum*, so abundant on the mountain heights of Europe, may serve as a type, develops a single flat umbel at the end of the stalk bearing flowers all hermaphrodite. They are also protogynous —their sticky stigmas can receive pollen, while their anthers are still closed. When flowering first begins, therefore, crossing can only be with other plants. Then the stamens straighten and stand out on all sides like a star till the long filaments place their anthers in the line of the neighbouring flowers. Since the stigmas are still receptive some of the pollen falling out of the bursting anthers inevitably reaches the stigmas of one of these flowers. The process which occurs in the umbel of *Siler* is but slightly different, although the flowers are exclusively protandrous, and not protogynous like those of *Pachypleurum*. In spite of this difference in the times of maturation the end attained is the same, as we shall see. The flowers in an umbel of *Siler* do not mature simultaneously like those of *Pachypleurum*, but the development proceeds very gradually from the circumference towards the centre of the umbel, so that the anthers of the central flowers do not dehisce until the outer ones have lost their pollen and matured their stigmas. Some of the crumbling pollen which falls out of the shrivelling anthers is now deposited on these ripening stigmas, since the thread-like filaments are long enough to reach to the middle of the outer flowers, and thus geitonogamy almost invariably ensues.

Both *Pachypleurum* and *Siler* and all the Umbelliferæ typified by them contain only hermaphrodite flowers in their umbels, and in this respect they differ from species of *Athamanta*, Spignel (*Meum*), and Chervil (*Chærophyllum*, see figs. 294[3] and 294[4], p. 320), whose umbels contain both hermaphrodite and staminate flowers like those of *Astrantia* and *Sanicula*. But this arrangement of the

flowers causes no alteration in the process of fertilization described. We would merely observe that in these plants the hermaphrodite flowers always open earlier than the staminate flowers of the same umbel. Not until the stamens of the hermaphrodite flowers have dehisced and fallen away, whilst their stigmas have been waiting for two days for pollen from other plants, do the anthers of the staminate flowers open after growing up far beyond their corollas. Their pollen then falls on the stigmas of the hermaphrodite flowers. Since there are so many more staminate than hermaphrodite flowers, the success of the process is doubly assured. For example, the umbel of *Chærophyllum aromaticum* (see figs. 294[3] and 294[4]) contains 20 staminate flowers besides one central and 3–5 peripheral hermaphrodite flowers, and therefore to 8–12 functional stigmas there are about 100 anthers. Moreover, the hermaphrodite flowers in these Umbelliferæ assume such a position at the moment the staminate flowers open that a pollination of their stigmas by the falling pollen is almost unavoidable (fig. 294[4]).

One of the most remarkable instances of geitonogamy is observed in such Umbelliferæ as the Beaked Parsley (*Anthriscus*), Fennel (*Fœniculum*), Coriander (*Coriandrum*), Water Parsnip (*Sium*), and *Ferulago*. All the species of these genera have two kinds of inflorescence. The umbels which blossom first contain principally true hermaphrodite flowers with a few isolated staminate flowers here and there; the later umbels consist only of staminate flowers. The hermaphrodite flowers which come first are completely protandrous; the anthers, borne on very thin filaments, are brought one after the other to the centre of the flower, where they dehisce and scatter their pollen, and the day following they drop off. After all the five stamens have dropped off the stigmas become mature and receptive. They continue in this condition for two days, and during this period are liable to crossing with the pollen of other plants. Then the umbels bearing only staminate flowers come under consideration. The pedicels which bear them have meanwhile elongated, and have thus obtained such a position that these umbels stand right over the hermaphrodite flowers with their mature stigmas, so that they seem to form an upper story, so to speak, in the inflorescence as a whole. Now, when the anthers in the staminate flowers of this upper story open, and when their walls shrivel up, the pollen is thrown out and falls vertically downwards in minute crumbling masses. The stigmas of the lower, older flowers are thus subjected to a rain of pollen, and it is easy to see that the majority of the stigmas are pollinated in this manner.

The instances of geitonogamy described in Compositæ and Umbelliferæ may be regarded as typical of what occurs in many representatives of other families. The Stellatæ section of Rubiaceæ, Caprifoliaceæ, Cornaceæ, Scrophulariaceæ, Rosaceæ, Polygonaceæ, Liliaceæ, and Aroideæ, whose flowers are crowded together in capitula, balls, fascicles, spikes, and racemes, repeat these processes sometimes down to the minutest detail. For example, the two styles in the protandrous fascicled flowers of a Woodruff, *Asperula taurina*, elongate, separate from each other and bend over just like those of *Laserpitium*; by this alteration of position they get into the

region of the younger flowers, where pollen is being shed, and their stigmas thus actually come into contact with the pollen. The process is still further promoted in this species of Woodruff by the fact that the last flowers to be produced are staminate. In the Red-berried Elder (*Sambucus racemosa*), various species of the Cornel and Dogwood genus (*Cornus florida, mas, sanguinea*), in the Vines (*Vitis*), which bear true hermaphrodite flowers, in the Tufted Loosestrife (*Lysimachia thyrsiflora*), and in many Spiræas (*Spiræa*), the arrangements for geitonogamy resemble those of *Siler trilobum* in that the direction of the style and the position of the stigma remain unaltered, but the filaments of the anthers elongate and bend over so as to deposit the pollen on the stigmas of adjacent flowers. In the Wayfaring-tree and Guelder-rose (*Viburnum Lantana, V. Opulus*) we have yet another contrivance—the pollen which is shed from the bent anthers of one flower falls to the bottom of the cup-shaped corolla of an adjacent one, where the large cushion-like stigma is situated.

The process of geitonogamy in the Snake-root (*Calla palustris*) and in *Saxifraga juniperifolia* to some extent resembles the fall of pollen in Compositæ. The flowers in these plants are crowded in short spikes or fascicles. They are protogynous, the stigma in the lower half of the inflorescence not ripening until the upper flowers are shedding their pollen. Now, when the anthers begin to shrivel and the pollen is thrown out, it necessarily falls on the fertile stigmas below. In those species of *Veronica* which have spicate inflorescences (*Veronica maritima, spicata, spuria*, &c.), the method of geitonogamy is slightly different, for here the style undergoes peculiar movements during the flowering period. The crowded flowers are all protogynous, and the stigmas of the flowers which first unfold are exposed to the pollen of plants of other species. This continues for two days. Meanwhile the stamens of the lowest flowers on the spike have elongated and pushed their anthers into the place first occupied by their stigmas; the anthers then dehisce and shed their pollen. But shortly before this the style has bent sharply downwards so that it is impossible for its stigmas to come in contact with this liberated pollen. Not until all the pollen has fallen down by the shrivelling up of the anthers or has been carried away by insects do the styles again straighten and project almost horizontally from the axis of the spike. The upper flowers on the spike undergo the same course of development, but the stages here are two days later. On this account the pollen falls from the anthers of the higher flowers just when the styles of the lower flowers again become straight. The still fresh stigmas at the ends of the styles thus come into line with the falling pollen and are efficiently pollinated by it.

A similar process occurs in *Eremurus* (see fig. 293 [2], p. 309), but here there is no fall of pollen. The stigmas at the end of the just straightened style are brought by their change of position directly into contact with the orange-yellow pollen still clinging to the withered anthers of the higher flowers. Many of the styles, of course, brush by the anthers without effecting this contact, and accordingly many stigmas in the racemes of *Eremurus* remain unpollinated. The transfer of the

pollen by insects occurs but seldom in this plant, so that from the many ovaries in the inflorescence of *Eremurus* usually only a few fruits are matured. This is the more remarkable as these flowers have remarkably long-lived stigmas, a peculiarity which is generally very advantageous in bringing about cross-pollination. The stigma is already mature when the perianth opens; when the tips of the perianth roll back and assume the form of aphides (see p. 171), and when the style moves like the hand of a watch towards the axis of the inflorescence, the stigma is still receptive, and remains so even when the style has again straightened and assumed an oblique upward direction.

A peculiar instance of geitonogamy is observed in *Allium Victorialis*. Each umbel is composed of flowers of very different ages. Before the first flowers bend over, wither, and shrivel up, their pollen-covered anthers project well over the edge of the perianth. In the younger flowers, at the same time, the anthers are still closed and covered by the perianth-leaves, but the stigmas are ripe and project beyond them. These young and hitherto short-stalked flowers are now raised by the elongation of their pedicels and inserted between the older flowers, so that, as a matter of course, their stigmas are brushed by the pollen of the older flowers, if it does not indeed fall on them.

The geitonogamy in the Bistort (*Polygonum Bistorta*) is very strange. It is rendered rather complex, as a peculiar distribution of the sexes is combined with a pronounced dichogamy and a peculiar way of opening. The inflorescence, which looks like a spike, is really composed of numbers of tiny two-flowered groups crowded together. One of the two flowers of each little group is long-styled and truly hermaphrodite, while the other contains a short style, well-formed stamens, and a rudimentary ovary which develops no further. It is therefore a pseudo-hermaphrodite staminate flower. In each group the long-styled hermaphrodite flower opens first, beginning at the base of the apparent spike and gradually working up to the top. The staminate flowers do not get their turn until the highest of the long-styled flowers has opened; but after this they behave exactly like their neighbours, i.e. the lowest develops first. The long-styled flowers are proterandrous. At the commencement of flowering the pollen-covered anthers project a millimetre from the perianth; the styles, however, are still short and hidden in the interior. At this time pollen can only be received from the flowers. Then the anthers fall off and the styles elongate so as to project some 5 mm. beyond the perianth. The whole spike is at this stage beset with receptive stigmas which can only be fertilized by insects with pollen from older plants. But this state of things does not last long for now the staminate flowers open one after another in quick succession. Their anthers containing abundance of pollen project 5 mm. beyond the perianth and come into contact with the still receptive stigmas of their neighbours, so that geitonogamy results. Even in this stage the staminate flowers become detached from the axis of the spike and fall to the ground. This geitonogamy is of course useless to the stigmas which have already received pollen from other plants by insect agency, but it is of the greatest importance to the flowers

which have not been so visited, for they would otherwise wither without being pollinated. In this sense we may regard the staminate flowers of *Polygonum Bistorta* as reserve flowers which, in case of absence of insect-visits, can come to the rescue in the last extremity with their own pollen.

Many plants related to the Bistort belonging to the Rhubarb and Dock genera (*Rheum*, *Rumex*), and many species of the Meadow-rue (*Thalictrum*) belonging to the Ranunculaceæ, agree for the most part with the case just described. The hermaphrodite flowers of the Rhubarb are protandrous. The anthers project, one after the other, above the edge of the tiny bell-shaped perianth, where they open and emit their floury pollen. This is easily shaken off by the least movement, and soon afterwards the anthers tumble off their filaments. At this time the three styles on the top of the ovary are bent back, and the large, swollen, cauliflower-like stigmas are so hidden at the base of the perianth that the pollen can gain no access to them. Not until all the anthers have fallen off do the styles straighten and place their succulent three-lobed stigmas in front of the edge of the perianth. Since the development of the extensive inflorescences of the Rhubarb takes place only gradually, one flower withering when another near it has just opened, the pollen shaken from the anthers of the younger flowers usually falls on the stigmas of the older ones. Sometimes the pseudo-hermaphrodite staminate flowers, which also occur in the inflorescence of the Rhubarb, and which are the last to open, have to provide the pollen for the adjoining hermaphrodite flowers, and after having performed their task they fall off. The course of development in the Alpine Dock (*Rumex alpinus*) gives rise to geitonogamy, but the process differs from that in the Rhubarb, since the stigmas do not emerge from their hiding-place in the depths of the perianth by the straightening of the style, but are rendered conspicuous by the folding back of the perianth-leaves, whilst in several Meadow-rues (*Thalictrum alpinum*, *fœtidum*, and *minus*) the stigmas, which are at first concealed under the petaline sepals, are exposed and rendered accessible to the pollen of neighbouring flowers by the falling away of the sepals which cover them.

These plants have floury pollen which, in the absence of wind, may fall vertically on the stigmas of neighbouring flowers, but whose transport is usually effected by breezes. They therefore afford a transition to such plants as have hermaphrodite flowers in which geitonogamy is chiefly brought about by the wind, although it may also result in the same way as in the Meadow-rues and the Docks and Rhubarbs. These plants were mentioned when we were considering the inadvisability of dividing plants into those which are respectively anemophilous and entomophilous (see p. 129). These plants would belong to both classes; at first they are insect-fertilized, and later on they are fertilized by the wind. The Mediterranean Heath (*Erica carnea*), which grows in Alpine districts from the valley-floor almost to the summits of limestone mountains, may be taken as the type of some two hundred Ericaceæ. This plant is much frequented by bees, and their visits are the cause of manifold crossings, sometimes between the flowers of the same plant, sometimes with other plants. In this plant, however, the crossing of neighbouring

flowers is more often effected by the wind. This process will be rendered clearer with the help of figs. 295 [1, 2, 3, 4]. The flowers are arranged in a row, with their mouths directed to one side pointing obliquely downwards (295 [1]). Flowering begins at the top of the branch, and then works gradually downwards. The stigma comes into sight simultaneously with the opening of the corolla, and protrudes some distance in front of its mouth by the elongation of the style. The anthers surrounding the style are still closed, and are either wholly or half hidden in the corolla (295 [2]). Bees coming to suck the honey at the base of the flower inevitably

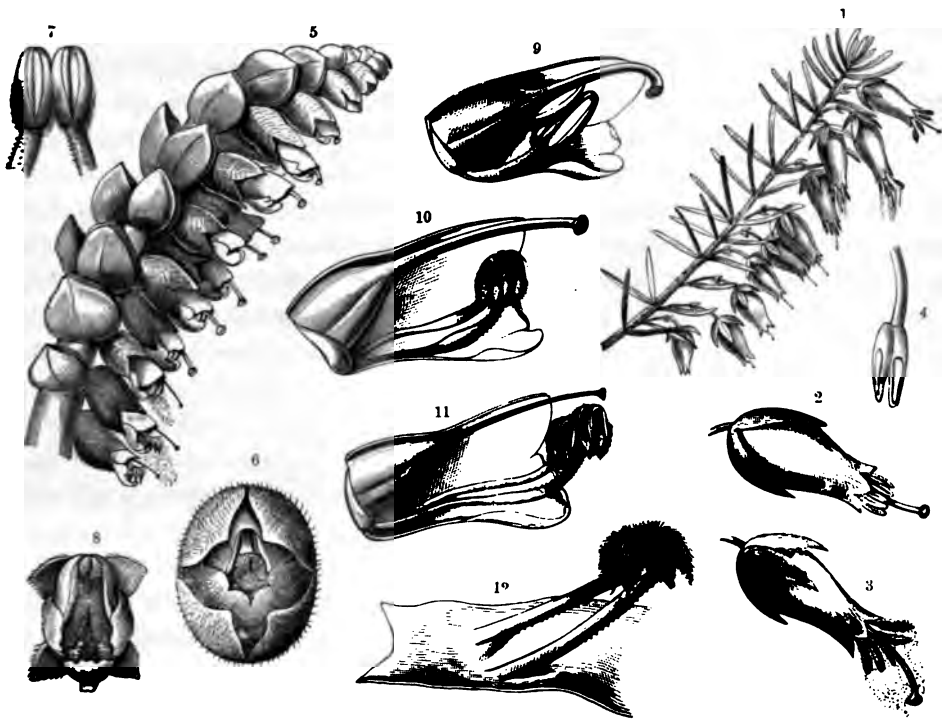

Fig. 295.—Geitonogamy with dust-like pollen.

[1] *Erica carnea*; branch with flowers on one side only. [2] Flower of the same in its first stage. [3] The same flower in its last stage. [4] Single stamen of *Erica carnea*. [5] *Lathræa Squamaria*; upper part of inflorescence. [6] Front view of a flower which has just opened. [7] Two anthers with closed loculi from the same flower. [8] Front view of a flower at a later stage. [9, 10, 11] Longitudinal sections of three flowers in the first, second, and third stages respectively. [12] Two anthers whose floury pollen has fallen, leaving empty loculi. [1] and [5] nat. size; the others somewhat enlarged.

brush against the stigma in consequence of its peculiar position. If they have brought pollen with them from other Heaths, a crossing between different plants is the result. Meanwhile large pores have formed in the anthers (see fig. 295 [4]). But since the pores on adjacent anthers are in immediate contact with one another, and since the anthers themselves are held together by the corolla (which is rather constricted at its mouth), as if by a ring, the pollen remains stored up in the anther-cavities and the pollen-tetrads do not fall out unless disturbed in some way. The anthers are disturbed whenever a bee inserts its proboscis into the flower in search of the honey, and therefore the same bee which at first brushed against the project-

agrees with *Sanicula* in having hermaphrodite and staminate flowers in each umbel, the hermaphrodite flowers developing first and being protogynous, so that again the sticky stigmas of the first-opened flowers in a given locality can only be fertilized by the pollen of other species. Later, the stigmas of the hermaphrodite flowers separate, and to a certain extent offer themselves to the pollen of the neighbouring staminate flowers which is now being shed. *Laserpitium* exhibits the same general arrangement of flowers as *Sanicula* and *Astrantia*, but the hermaphrodite flowers in the large, loose umbel are protandrous instead of protogynous. Geitonogamy, however, obtains, just as in *Astrantia*, by the stigmas at the top of the divided style exposing themselves to the pollen from the anthers of the neighbouring staminate flowers. Since the protandrous hermaphrodite flowers open before the staminate ones, their stigmas are mature exactly at the same time that the anthers of the latter shed their pollen.

A notable exception to these Umbelliferæ which have been described, where the stigmas of one flower obtain the pollen from neighbouring flowers by the elongation and bending of their styles into their neighbour's domain, thus producing geitonogamy, is afforded by others whose styles and stigmas retain their original position. The stamens, however, elongate and straighten, and assume such a position that the pollen liberated from their anthers can reach the stigmas of the neighbouring flowers. One group of such species, of which *Pachypleurum*, so abundant on the mountain heights of Europe, may serve as a type, develops a single flat umbel at the end of the stalk bearing flowers all hermaphrodite. They are also protogynous —their sticky stigmas can receive pollen, while their anthers are still closed. When flowering first begins, therefore, crossing can only be with other plants. Then the stamens straighten and stand out on all sides like a star till the long filaments place their anthers in the line of the neighbouring flowers. Since the stigmas are still receptive some of the pollen falling out of the bursting anthers inevitably reaches the stigmas of one of these flowers. The process which occurs in the umbel of *Siler* is but slightly different, although the flowers are exclusively protandrous, and not protogynous like those of *Pachypleurum*. In spite of this difference in the times of maturation the end attained is the same, as we shall see. The flowers in an umbel of *Siler* do not mature simultaneously like those of *Pachypleurum*, but the development proceeds very gradually from the circumference towards the centre of the umbel, so that the anthers of the central flowers do not dehisce until the outer ones have lost their pollen and matured their stigmas. Some of the crumbling pollen which falls out of the shrivelling anthers is now deposited on these ripening stigmas, since the thread-like filaments are long enough to reach to the middle of the outer flowers, and thus geitonogamy almost invariably ensues.

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One of the most remarkable instances of geitonogamy is observed in such Umbelliferæ as the Beaked Parsley (*Anthriscus*), Fennel (*Fœniculum*), Coriander (*Coriandrum*), Water Parsnip (*Sium*), and *Ferulago*. All the species of these genera have two kinds of inflorescence. The umbels which blossom first contain principally true hermaphrodite flowers with a few isolated staminate flowers here and there; the later umbels consist only of staminate flowers. The hermaphrodite flowers which come first are completely protandrous; the anthers, borne on very thin filaments, are brought one after the other to the centre of the flower, where they dehisce and scatter their pollen, and the day following they drop off. After all the five stamens have dropped off the stigmas become mature and receptive. They continue in this condition for two days, and during this period are liable to crossing with the pollen of other plants. Then the umbels bearing only staminate flowers come under consideration. The pedicels which bear them have meanwhile elongated, and have thus obtained such a position that these umbels stand right over the hermaphrodite flowers with their mature stigmas, so that they seem to form an upper story, so to speak, in the inflorescence as a whole. Now, when the anthers in the staminate flowers of this upper story open, and when their walls shrivel up, the pollen is thrown out and falls vertically downwards in minute crumbling masses. The stigmas of the lower, older flowers are thus subjected to a rain of pollen, and it is easy to see that the majority of the stigmas are pollinated in this manner.

The instances of geitonogamy described in Compositæ and Umbelliferæ may be regarded as typical of what occurs in many representatives of other families. The Stellatæ section of Rubiaceæ, Caprifoliaceæ, Cornaceæ, Scrophulariaceæ, Rosaceæ, Polygonaceæ, Liliaceæ, and Aroideæ, whose flowers are crowded together in capitula, balls, fascicles, spikes, and racemes, repeat these processes sometimes down to the minutest detail. For example, the two styles in the protandrous fascicled flowers of a Woodruff, *Asperula taurina*, elongate, separate from each other and bend over just like those of *Laserpitium*; by this alteration of position they get into the

region of the younger flowers, where pollen is being shed, and their stigmas thus actually come into contact with the pollen. The process is still further promoted in this species of Woodruff by the fact that the last flowers to be produced are staminate. In the Red-berried Elder (*Sambucus racemosa*), various species of the Cornel and Dogwood genus (*Cornus florida, mas, sanguinea*), in the Vines (*Vitis*), which bear true hermaphrodite flowers, in the Tufted Loosestrife (*Lysimachia thyrsiflora*), and in many Spiræas (*Spiræa*), the arrangements for geitonogamy resemble those of *Siler trilobum* in that the direction of the style and the position of the stigma remain unaltered, but the filaments of the anthers elongate and bend over so as to deposit the pollen on the stigmas of adjacent flowers. In the Wayfaring-tree and Guelder-rose (*Viburnum Lantana, V. Opulus*) we have yet another contrivance—the pollen which is shed from the bent anthers of one flower falls to the bottom of the cup-shaped corolla of an adjacent one, where the large cushion-like stigma is situated.

The process of geitonogamy in the Snake-root (*Calla palustris*) and in *Saxifraga juniperifolia* to some extent resembles the fall of pollen in Compositæ. The flowers in these plants are crowded in short spikes or fascicles. They are protogynous, the stigma in the lower half of the inflorescence not ripening until the upper flowers are shedding their pollen. Now, when the anthers begin to shrivel and the pollen is thrown out, it necessarily falls on the fertile stigmas below. In those species of *Veronica* which have spicate inflorescences (*Veronica maritima, spicata, spuria*, &c.), the method of geitonogamy is slightly different, for here the style undergoes peculiar movements during the flowering period. The crowded flowers are all protogynous, and the stigmas of the flowers which first unfold are exposed to the pollen of plants of other species. This continues for two days. Meanwhile the stamens of the lowest flowers on the spike have elongated and pushed their anthers into the place first occupied by their stigmas; the anthers then dehisce and shed their pollen. But shortly before this the style has bent sharply downwards so that it is impossible for its stigmas to come in contact with this liberated pollen. Not until all the pollen has fallen down by the shrivelling up of the anthers or has been carried away by insects do the styles again straighten and project almost horizontally from the axis of the spike. The upper flowers on the spike undergo the same course of development, but the stages here are two days later. On this account the pollen falls from the anthers of the higher flowers just when the styles of the lower flowers again become straight. The still fresh stigmas at the ends of the styles thus come into line with the falling pollen and are efficiently pollinated by it.

A similar process occurs in *Eremurus* (see fig. 293 [2], p. 309), but here there is no fall of pollen. The stigmas at the end of the just straightened style are brought by their change of position directly into contact with the orange-yellow pollen still clinging to the withered anthers of the higher flowers. Many of the styles, of course, brush by the anthers without effecting this contact, and accordingly many stigmas in the racemes of *Eremurus* remain unpollinated. The transfer of the

pollen by insects occurs but seldom in this plant, so that from the many ovaries in the inflorescence of *Eremurus* usually only a few fruits are matured. This is the more remarkable as these flowers have remarkably long-lived stigmas, a peculiarity which is generally very advantageous in bringing about cross-pollination. The stigma is already mature when the perianth opens; when the tips of the perianth roll back and assume the form of aphides (see p. 171), and when the style moves like the hand of a watch towards the axis of the inflorescence, the stigma is still receptive, and remains so even when the style has again straightened and assumed an oblique upward direction.

A peculiar instance of geitonogamy is observed in *Allium Victorialis*. Each umbel is composed of flowers of very different ages. Before the first flowers bend over, wither, and shrivel up, their pollen-covered anthers project well over the edge of the perianth. In the younger flowers, at the same time, the anthers are still closed and covered by the perianth-leaves, but the stigmas are ripe and project beyond them. These young and hitherto short-stalked flowers are now raised by the elongation of their pedicels and inserted between the older flowers, so that, as a matter of course, their stigmas are brushed by the pollen of the older flowers, if it does not indeed fall on them.

The geitonogamy in the Bistort (*Polygonum Bistorta*) is very strange. It is rendered rather complex, as a peculiar distribution of the sexes is combined with a pronounced dichogamy and a peculiar way of opening. The inflorescence, which looks like a spike, is really composed of numbers of tiny two-flowered groups crowded together. One of the two flowers of each little group is long-styled and truly hermaphrodite, while the other contains a short style, well-formed stamens, and a rudimentary ovary which develops no further. It is therefore a pseudo-hermaphrodite staminate flower. In each group the long-styled hermaphrodite flower opens first, beginning at the base of the apparent spike and gradually working up to the top. The staminate flowers do not get their turn until the highest of the long-styled flowers has opened; but after this they behave exactly like their neighbours, *i.e.* the lowest develops first. The long-styled flowers are protandrous. At the commencement of flowering the pollen-covered anthers project a millimetre from the perianth; the styles, however, are still short and hidden in the interior. At this time pollen can only be removed from the flowers. Then the anthers fall off and the styles elongate so as to protrude some 3 mm. beyond the perianth. The whole spike is at this stage beset with receptive stigmas which can only be fertilized by insects with pollen from other plants. But this state of things does not last long, for now the staminate flowers open one after another in quick succession. Their anthers, containing abundance of pollen, protrude 3 mm. beyond the perianth and come into contact with the still receptive stigmas of their neighbours, so that geitonogamy results. As soon as this is effected the staminate flowers become detached from the axis of the spike and fall to the ground. This geitonogamy is of course useless to the stigmas which have already received pollen from other plants by insect agency, but it is of the greatest importance to the flowers

which have not been so visited, for they would otherwise wither without being pollinated. In this sense we may regard the staminate flowers of *Polygonum Bistorta* as reserve flowers which, in case of absence of insect-visits, can come to the rescue in the last extremity with their own pollen.

Many plants related to the Bistort belonging to the Rhubarb and Dock genera (*Rheum, Rumex*), and many species of the Meadow-rue (*Thalictrum*) belonging to the Ranunculaceæ, agree for the most part with the case just described. The hermaphrodite flowers of the Rhubarb are protandrous. The anthers project, one after the other, above the edge of the tiny bell-shaped perianth, where they open and emit their floury pollen. This is easily shaken off by the least movement, and soon afterwards the anthers tumble off their filaments. At this time the three styles on the top of the ovary are bent back, and the large, swollen, cauliflower-like stigmas are so hidden at the base of the perianth that the pollen can gain no access to them. Not until all the anthers have fallen off do the styles straighten and place their succulent three-lobed stigmas in front of the edge of the perianth. Since the development of the extensive inflorescences of the Rhubarb takes place only gradually, one flower withering when another near it has just opened, the pollen shaken from the anthers of the younger flowers usually falls on the stigmas of the older ones. Sometimes the pseudo-hermaphrodite staminate flowers, which also occur in the inflorescence of the Rhubarb, and which are the last to open, have to provide the pollen for the adjoining hermaphrodite flowers, and after having performed their task they fall off. The course of development in the Alpine Dock (*Rumex alpinus*) gives rise to geitonogamy, but the process differs from that in the Rhubarb, since the stigmas do not emerge from their hiding-place in the depths of the perianth by the straightening of the style, but are rendered conspicuous by the folding back of the perianth-leaves, whilst in several Meadow-rues (*Thalictrum alpinum, fœtidum*, and *minus*) the stigmas, which are at first concealed under the petaline sepals, are exposed and rendered accessible to the pollen of neighbouring flowers by the falling away of the sepals which cover them.

These plants have floury pollen which, in the absence of wind, may fall vertically on the stigmas of neighbouring flowers, but whose transport is usually effected by breezes. They therefore afford a transition to such plants as have hermaphrodite flowers in which geitonogamy is chiefly brought about by the wind, although it may also result in the same way as in the Meadow-rues and the Docks and Rhubarbs. These plants were mentioned when we were considering the inadvisability of dividing plants into those which are respectively anemophilous and entomophilous (see p. 129). These plants would belong to both classes; at first they are insect-fertilized, and later on they are fertilized by the wind. The Mediterranean Heath (*Erica carnea*), which grows in Alpine districts from the valley-floor almost to the summits of limestone mountains, may be taken as the type of some two hundred Ericaceæ. This plant is much frequented by bees, and their visits are the cause of manifold crossings, sometimes between the flowers of the same plant, sometimes with other plants. In this plant, however, the crossing of neighbouring

flowers is more often effected by the wind. This process will be rendered clearer with the help of figs. 295 [1, 2, 3, 4]. The flowers are arranged in a row, with their mouths directed to one side pointing obliquely downwards (295 [1]). Flowering begins at the top of the branch, and then works gradually downwards. The stigma comes into sight simultaneously with the opening of the corolla, and protrudes some distance in front of its mouth by the elongation of the style. The anthers surrounding the style are still closed, and are either wholly or half hidden in the corolla (295 [2]). Bees coming to suck the honey at the base of the flower inevitably

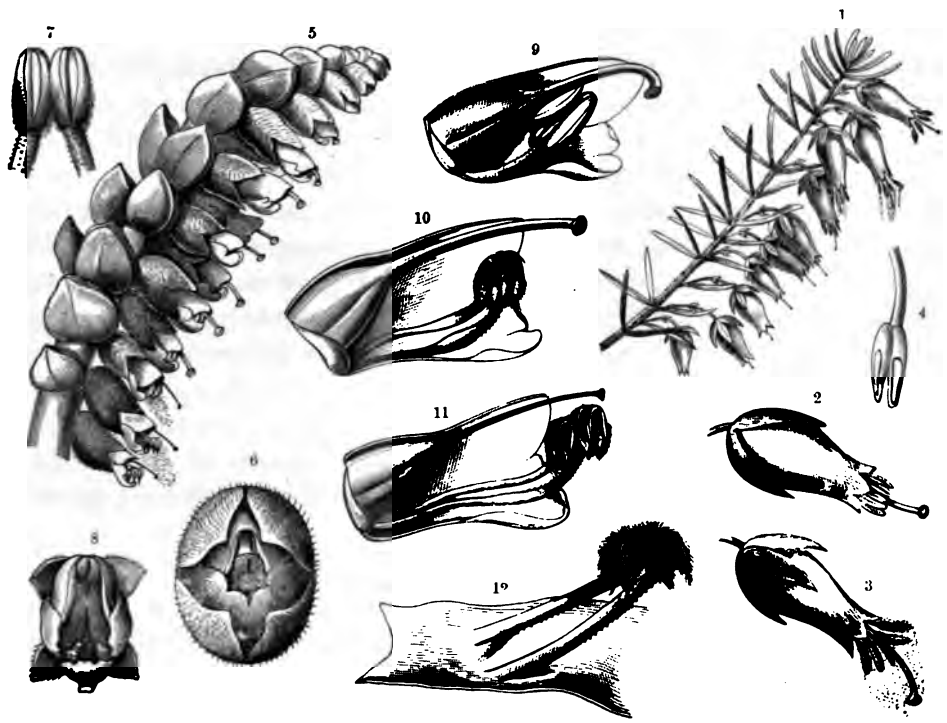

Fig. 295.—Geitonogamy with dust-like pollen.

[1] *Erica carnea*; branch with flowers on one side only. [2] Flower of the same in its first stage. [3] The same flower in its last stage. [4] Single stamen of *Erica carnea*. [5] *Lathræa Squamaria*; upper part of inflorescence. [6] Front view of a flower which has just opened. [7] Two anthers with closed loculi from the same flower. [8] Front view of a flower at a later stage. [9, 10, 11] Longitudinal sections of three flowers in the first, second, and third stages respectively. [12] Two anthers whose floury pollen has fallen, leaving empty loculi. [1] and [5] nat. size; the others somewhat enlarged.

brush against the stigma in consequence of its peculiar position. If they have brought pollen with them from other Heaths, a crossing between different plants is the result. Meanwhile large pores have formed in the anthers (see fig. 295 [4]). But since the pores on adjacent anthers are in immediate contact with one another, and since the anthers themselves are held together by the corolla (which is rather constricted at its mouth), as if by a ring, the pollen remains stored up in the anther-cavities and the pollen-tetrads do not fall out unless disturbed in some way. The anthers are disturbed whenever a bee inserts its proboscis into the flower in search of the honey, and therefore the same bee which at first brushed against the project-

ing stigma is, in the next instant, smothered in pollen over its proboscis, head, and thorax. Cross-pollination must ensue if this bee shortly after visits the flowers of another plant, and wherever Heaths which flower simultaneously grow together there is no lack of hybridization. Whether the stigma of a flower is pollinated by bees with pollen of another plant of the same or of another species or not at all, it always begins to wither in two days' time and ceases to be receptive. The stamens in the same flower now elongate and push their anthers out of the corolla mouth. The restriction being removed the anthers separate, and pollen will fall out of their compartments at the slightest movement (see fig. 295 [3]). The merest swaying of the flowering branch is sufficient to cause the pollen to fall. The still receptive sticky stigmas of the younger flowers on the same branch, and indeed of flowers on other branches of the same plant at some distance, are thus necessarily pollinated with the dust-like pollen.

In the inflorescence of the Toothwort (*Lathræa Squamaria*) the crossing is effected in exactly the same way. The flowers, like those of the Heath, are all turned towards the side from which insects may be expected to arrive (see fig. 295 [5]). They are protogynous, and the ripe stigma projects beyond the margin of the corolla before the latter has properly opened and when the anthers below are still closed (see figs. 295 [6, 7, 9]). At this stage the stigma can only be pollinated with the pollen of other plants whose development is further advanced. Corolla, style, and filaments continue to elongate, the style, which has hitherto been bent like a hook, straightens, the stigma, which was formerly in front of the narrow entrance to the flower, takes a higher position, the anthers dehisce, and the flower now enters upon its second stage (see figs. 295 [8] and 295 [10]). Pollination is effected at this time by insects. Humble-bees suck the honey secreted by a succulent cushion below the ovary, and so transfer the pollen of the Toothwort from flower to flower. When they come to a flower they brush against the projecting stigma and deposit pollen on it which they have gathered elsewhere; they then push their probosces between the anthers, which are held together by soft hairs. They are obliged to take this path, for otherwise they would soon come to grief. The filaments below the anthers are studded with little pointed thorns (see fig. 295 [10]), and the humble-bee carefully avoids any contact with them. He therefore passes between the contiguous anthers of the sprinkling stamens (*cf.* p. 271), separating them slightly, and thus causing a fall of dusty pollen which covers his proboscis and head. And now comes the third and last stage. The style and stigma wither and dry up, and the stamens elongate and push their anthers beyond the margin of the corolla (see figs. 295 [11] and 295 [12]). The anthers no longer cohere. The pollen retained in their cavities is carried away by the wind, and will be deposited in part on the still receptive stigmas of neighbouring, younger flowers. If a flower has already been visited by a humble-bee very little pollen will remain in its anthers, but if there has been no insect-visit the anthers are full of pollen when they are extended from the flower, and this is wafted in small clouds to the stigmas of the younger flowers in the upper part of the spike. Here again, as in so many instances, geitonogamy does not supervene till towards

the close of flowering. At first the plant seems to offer facilities for hybridization, later for a crossing of different plants of the same species, and not until both these processes have failed, owing to lack of insect-visits, does it fall back on cross-pollination between neighbouring flowers of the same plant. The processes and contrivances in the flowers of *Clandestina rectiflora*, *Bartsia alpina* and of some other Rhinanthaceæ agree in the main with those of the Toothwort, so that there is no need to describe them in detail. In conclusion, the Persian *Crucianella stylosa*, one of the Stellatæ group of the Rubiaceæ, must be considered especially with regard to the geitonogamy of its hermaphrodite flowers. This plant has already been mentioned (pp. 265, 267), and it was stated that the tips of the corolla-lobes formed a hollow cone which at a touch suddenly burst open, scattering the pollen hidden beneath (fig. 272). If an insect is the cause of the disturbance it becomes covered with the liberated pollen, and should it then visit other flowers of this same *Crucianella* it is not too much to say that the pollen it carries on its body will be deposited on the stigmatic tissue at the thickened end of the slender styles projecting far above the corolla (see fig. 272[5]). If the flower is not visited, however, it will burst open and scatter its pollen spontaneously. The dust-like pollen is then diffused into the surrounding air, and so easily reaches the ripe stigmas of the neighbouring flowers.

AUTOGAMY.

By the term *Autogamy* is understood the transference of pollen from the stamens to the stigmas of the same flower, in other words—*self-pollination*. Autogamy can, therefore, only occur in hermaphrodite flowers, but it must not be inferred that the only method of reproduction in hermaphrodite flowers is by autogamy. In the last chapter we showed the error into which Linnæus fell by making this assumption, and referred to the almost interminable list of contrivances to bring about cross-pollination in hermaphrodite flowers between different species, between different individuals of the same species, and between flowers on the same individual. This important result of modern investigation has led not only to a correction of the views of the celebrated Swedish Botanist, but to the belief that autogamy is avoided in the vegetable world. Darwin even held the opinion that there must be something injurious in autogamy to account for the number of obstacles placed in its way. This statement, though commonly made in text-books as embodying a law of nature, is, however, not a correct expression of the facts observed. It is true that cross-pollination appears to be the primary object aimed at, but it is not true that autogamy is avoided. If cross-pollination takes place there is naturally no necessity for subsequent autogamy, but if cross-pollination fails autogamy assumes an importance of its own, and the contrivances which have been observed to bring about autogamy are no less numerous than those which favour cross-pollination. That flowers should be adapted at different times to two such diverse purposes as cross- and self-pollination is one of the marvels of floral construction.

As the above conclusion forms the main basis of the theory concerning the origin of species to be presently unfolded, some preliminary account of the observations on which it is founded must now be given, but the task is not an easy one. For five-and-twenty years I have been studying, with special reference to the phenomena in question, the flowers of many more than a thousand species in all stages of development from budding to fruiting, some growing wild in their original habitats, some in the Gardens under my direction, and my notes are so numerous that even the briefest outline of the cases observed would fill several volumes. I must, therefore, content myself with presenting the different instances in groups according to their degrees of similarity. Even the number of groups, however, is surprisingly large, and only their general description can be attempted. The best way will be to select a representative species for each kind of adaptation that we have to deal with, and to point out in a few words its more important characteristics. As the processes to be described as taking place during the flowering period all tend to the same result though differing greatly in other ways, and as the terms used must be applied over and over again to the phenomena which are common to all the cases, it is impossible to avoid a certain monotony in the descriptions that follow, and the reader is begged to exercise some patience in the perusal of this chapter.

The simplest case of autogamy occurs as follows. The flower opens revealing the stigma stationed in front of the entrance to the receptacle and already mature, whilst the anthers are closely adherent to the stigma but are still closed. Autogamy is, for the time, impossible, whereas cross-pollination may be effected through the intervention of wind or insects. In the second half of the flowering-period the anthers adjacent to the stigma open, and the stigma is instantly covered with the pollen set free from them. There are only a few varieties of this simplest case of autogamy worth mentioning. It has been observed to occur in particular in annual plants with small flowers (e.g. *Centunculus minimus*, *Geranium pusillum*, *Lithospermum arvense*), and again in several bulbous plants belonging to the section of Liliflorеæ, *e.g.* several species of *Fritillaria* and *Narcissus*, all the species of *Trillium* and *Uvularia*, and in a few species of *Crocus*. In *Trillium grandiflorum* and *Uvularia grandiflora*, two anthers are stationed in each of the three angles of the spreading stigmas, and in the process of autogamy only the pollen from that half of the anther which is turned inwards is used, whilst the pollen from the outward-facing halves of the anthers may be carried away by insects, even after autogamy has taken place. In the Crown Imperial (*Fritillaria imperialis*) only the pollen from the three longer stamens falls upon the stigma of the same flower. There are six stamens in the flowers of this plant, three of which are longer than the rest and alone have their anthers appressed to the tridentate stigma. These anthers open a day later than the others. Dehiscence is accompanied by a very considerable shrivelling and shortening of the anthers, and the result of this contraction is that the liberated pollen is scraped off the anthers by the edges of the stigmatic lobes. In *Crocus albiflorus*, which covers alpine meadows in early spring with its blossoms, the anthers at first rest with their arched backs in

contact with the stigma. The loculi, full of adhesive pollen, face outwards, and are so placed that insects coming in quest of honey must rub off the pollen emerging from their slits. The stigmas, on the other hand, assume such a position that the insects are obliged to touch their receptive tissue before brushing the anthers. Owing to the relative positions of stigmas and anthers cross-pollination is no doubt effected by insects in a large number of cases, and as only the backs of the anthers rest upon the stigma autogamy is, for the time, impossible. But towards the close of the flowering period the anthers are twisted round, with the result that the pollen of each loculus touches the stigma. Another circumstance contributory to this autogamy is that during the time of flowering the perianth-tube elongates from 5 to 15 mm., and the filaments, which are adnate to the perianth, from 3 to 4 mm. The anthers are in consequence pushed past the stigmatic margins and leave more pollen upon them than would otherwise be the case.

Convolvulus Sîculus, a native of the shores of the Mediterranean, may be taken as a type of several annual Bindweeds wherein the style bifurcates into two narrow filiform branches of considerable length which bear the receptive tissue and represent stigmas. One of these stigmas is erect, and continues the style in a straight line, whilst the other stands away at an angle of 60°, and forms a barrier in front of the approach to the floral receptacle. The stamens are adherent to the style, and at the time that the corolla opens the anthers rest against the erect stigma. At the period of dehiscence the anthers face outwards so that the upright stigma encompassed by them cannot receive their pollen when the flower first opens. On the other hand, the position of the anthers is favourable to the abstraction of pollen by insects seeking the honey in the interior of the flower. Later on, when the anthers shrivel they become covered all over with pollen, and then it is that a portion of it is transferred to the erect stigma, thus effecting autogamy. The second stigma, which lies across the entrance, seldom has pollen from the anthers of the same flower affixed to it; but pollen conveyed from other flowers is rubbed off insects on to this stigma, so that here we have an instance in which one stigma is adapted to autogamy and another to cross-pollination.

The process of autogamy occurs in pendent flowers, the anthers of which are joined together in a central cone, through a relaxation of the filaments towards the close of the flowering period, in consequence of which the loculi full of pollen no longer close together so tightly as before. The mealy pollen falls from the dislocated cone upon the stigma, which is still in a viscid and receptive condition. As types of this category of plants we may take the Snowdrop (*Galanthus*), *Soldanella*, of which previous mention has been made (see fig. 278 [1], p. 275), and *Dodecatheon*, which is allied to *Soldanella*, but in respect of the form of its flowers resembles *Cyclamen*. During the first part of their flowering-period they are adapted to cross-fertilization. The style projects far beyond the cone of anthers. Insects in search of honey begin by brushing against the stigma and then for a moment dislocate the anthers, letting a sprinkling of pollen fall on their heads. On visiting other flowers they rub this pollen on to the stigmas and so promote cross-fertilization. If, however, no insects

visit a flower, the anthers are still full of pollen at the close of its flowering period, and being then displaced let fall their pollen upon the slightest vibration of the pendent blossom, or even when it is quite still. The pollen falls straight down and is caught by the stigma below.

The process above described is only observed to take place in pendent flowers where the pollen is of floury consistency and the stamens are united into a conical cap. Flowers borne on horizontal stalks, and facing sideways, may exhibit the same phenomenon in connection with separate stamens. Only an important circumstance in this case is that some of the anthers should be exactly over the stigmas at the time of dehiscence. With a view to cross-fertilization, lateral flowers of the kind are protogynous, and have their anthers closed when the buds open; but later on the anthers dehisce, and a portion of the pollen then liberated falls out, owing to the contraction of the walls of the anthers, and besprinkles the stigma of the same flower. This method of autogamy has been observed in particular in the flowers of *Tofieldia* and the Bog Asphodel (*Narthecium*).

Even in upright flowers autogamy sometimes takes place in the second half of their time of flowering through a fall of pollen, and that without any change of position on the part of petals, stamens, or style. To make cross-fertilization possible, in the first instance, flowers of this kind are protogynous. Subsequently, after the dehiscence of the anthers, a portion of the crumbly pollen becomes detached, and is deposited on the stigma below. In the case of erect flowers with funnel-shaped corollas, the pollen slips down the smooth sloping wall of the funnel to the stigma, and it is not essential for the anthers to stand vertically above the stigma, since the corolla acts as a sort of conduit for the pollen. The Lilac (*Syringa*) is an example of the plants of this category. It is also remarkable for the fact that, though its flowers are only protogynous for a very short time, yet, for one or two days after the dehiscence of the anthers, autogamy cannot take place, because the anthers face outwards. So long as the anthers are in this position the pollen cannot be transferred without extraneous aid to the corolla-tube; it is not till later on, when the anthers get covered all round with pollen, owing to the gradual shrinkage of their walls, that some of the pollen drops on to the stigma standing underneath in the tube of the funnel.

Very often in erect or obliquely ascending flowers autogamy is brought about by an elongation of the filaments during the period of flowering, the result being that the anthers, which are originally lower down than the stigmas, are elevated to the same level as the latter, and are thus enabled to deposit their pollen upon them. Most of the species belonging to this group are protogynous; the filaments are erect, and are either adherent or else parallel to the ovary or style. At first the anthers are so far from the stigma that the pollen would not of itself dust the stigma in the same flower, but the subsequent elongation of the filaments is so regulated as to carry the anthers to the same level as the stigma by the time they are coated with pollen. The anthers then adhere to the receptive stigmatic tissue, and autogamy is the result. The following are instances of plants

in which this is observed to occur:—the Moschatel (*Adoxa Moschatellina*), most of the species of the Knawel (*Scleranthus*), *Pœderota Bonarota*, of wide distribution in the Southern Alps, the curious *Aponogeton distachyon*, native to South Africa, and a large number of Cruciferæ, Saxifragaceæ, Willow-herbs, Geraniaceæ, Convolvulaceæ, and Caryophyllaceæ.

Of the large family of the Cruciferæ we may mention *Arabis cærulea*, *Braya alpina*, *Cardamine alpina*, and *Rhizobotrya alpina*, all of which are small-flowered species growing in the upland hollows of high mountains, and in addition the annual or biennial species named *Lepidium campestre*, *L. sativum*, *Sisymbrium Alliaria*, *S. Thalianum*, *Thlaspi alliaceum* and *Thlaspi arvense*. In these plants the stigma is sessile on the ovary in the shape of a small round cushion, which becomes visible the moment the imbricate petals of the bud begin to move apart. At this period only cross-pollination can take place, as all the anthers in the flower itself are still closed; but the four long stamens now grow up along the wall of the ovary until the anthers are exactly on the same level as the stigma. The anthers have dehisced by that time, and their pollen cannot but be deposited on the receptive cells at the periphery of the stigmatic cushion. Another observation which has been repeatedly confirmed, is that only one of the four anthers parts with its pollen to the adjacent stigma, while the rest, though quite close to the stigma, are not in immediate contact with it. The pollen of these three anthers is apparently placed there so that it may be carried off by the small flies which visit these cruciferous plants and transferred by them to younger blossoms.

The Saxifrages (e.g. *Saxifraga androsacea*) here in question have two linear or oblong stigmas. After the anthers are raised, the pollen is usually brushed off them on to the sides of the stigma near its base. But here again it is noteworthy that for the most part only one of the five anthers devotes its pollen to the process of autogamy, whilst the others remain a little below the stigmas, and do not come into contact with them.

In a number of small-flowered Willow-herbs (*Epilobium collinum*, *E. montanum*, *E. parviflorum*, &c.) the stigma is composed of four thickish divergent lobes arranged in a cross with four angles between them. Upon the first parting of the petals, which always happens early in the morning, the anthers may be seen to be underneath the mature cruciform stigma, but in the course of that very day the filiform filaments grow to a sufficient length to place the anthers in the re-entrant angles of the cross. Meanwhile, dehiscence has taken place, and by the evening of the first day autogamy ensues. During the night the petals close up, and the flower droops a little; the next morning the petals open again, and it is then evident that the filaments have grown rather longer, two or three pollen-covered anthers standing above the stigma and partially concealing it. The place occupied by the stigma on the previous day is now filled by an assemblage of anthers laden with pollen, which is brushed off by insects and transported to other flowers. Thus we find in these Willow-herbs that on the first morning cross-fertilization

alone is possible, in the evening of the first day autogamy takes place, and on the next day pollen is again supplied to fertilize younger flowers—an alternation which clearly shows that autogamy is not invariably merely a last stage in the phenomenon of flowering.

Similar events occur in several small-flowered species of the Crane's Bill (e.g. *Geranium columbinum*, *G. lucidum*, *G. Robertianum*). In the middle of the newly-opened flower is a receptive stigma with five radiating arms, and around it are ten stamens, all of which are still closed. Five of the stamens are longer than the rest, and hold their anthers nearly on a level with the stigma; the other five anthers form a belt underneath the stigma. By the evening of the first day the anthers of the longer stamens are already open, and transfer their pollen to the tips of the adjacent stigmatic lobes. In *Geranium lucidum* the phenomenon is not even delayed till the evening, but takes place four hours after the flowers open. The flowers are not, however, then over. They close for the night, and nod or droop to protect the pollen (see figs. 225[1] and 225[2], p. 121), but next morning they again become erect. The five stamens standing in front of the petals then grow until the anthers reach the niches between the radiating lobes of the stigma, whereupon there is a transference of pollen to these lobes. Some of the anthers are afterwards lifted still higher, evidently for the purpose of dispersing, by aid of insects, such portion of the pollen as has not been applied to the process of autogamy.

Several Convolvulaceæ, of which the well-known *Ipomœa purpurea* is a type, have only two or three of their five stamens adapted to autogamy. The stamens, which are parallel to the style and usually adherent to it, are of unequal length, the shortest being 9 mm., the longest 17 mm., and the others 11 mm., 13 mm., and 15 mm. in length respectively. The anthers consequently stand at different heights and at the same time they are so disposed relatively as not to cover one another, an arrangement which has the advantage of presenting a comparatively large expanse of pollen along the passage leading to the honey in the interior of the flower. But even the anther of the longest stamen is 3 mm. lower than the stigma when the flower first opens. Owing to this arrangement and to the circumstance that the flowers are protogynous, only cross-fertilization through the intervention of insects can take place at the commencement of their flowering period. Later on, however, there is a lengthening of the stamens and the anthers pertaining to the longest two or three reach the same level as the stigma, and yield up their pollen to it. The process of autogamy is further facilitated by the involution of the corolla, which occurs at the close of flowering, whereby the anthers coated with pollen are pressed against the stigma.

From these Convolvulaceæ we pass to a long series of protandrous Caryophyllaceæ, mostly annual plants, such as *Agrostemma Githago*, *Saponaria Vaccaria*, and *Silene conica*, in which the anthers are brought into contact with the stigmas by a similar elongation of the stamens. The various changes occurring in flowers of the kind ensue with great regularity as follows:—(1) The petals separate, leaving

the approach to the floral receptacle open. Dehiscence has already taken place in the case of the anthers of the stamens inserted in front of the sepals, and their pollen is available for cross-fertilization by means of insects, but not for autogamy, owing to the fact that the receptive tissue of the style in the same flower is still inaccessible. (2) The anthers of the stamens inserted in front of the sepals drop off, or else their filaments become reflexed and are exserted beyond the periphery of the flower. The styles move asunder and arrange themselves like the spokes of a wheel in the middle of the flower, where they are liable to be covered with pollen brought by insects from other blossoms. The anthers of the stamens inserted in front of the petals are still closed. (3) Owing to a growth of the erect filaments of the last-mentioned stamens, their anthers are brought to the same height as and in direct contact with the spreading stigmas. Dehiscence ensues, and the liberated pollen is deposited on the receptive stigmatic tissue. In annual caryophyllaceous plants—*e.g.* in *Silene conica*—the whole process takes place in the course of a single day, whereas in the perennial *Dianthus glacialis* it occupies five or six days, or, if the weather is bad, from seven to nine days.

One of the commonest contrivances for effecting autogamy is the following. Anthers and stigmas stand at the same height, though, owing to the position and direction of the filaments, the anthers are so far from the stigma that no transference of the adhesive pollen to it can take place. At the proper moment, however, the straight and rigid filiform filaments perform certain special movements with the object of conveying pollen from the anthers to the stigma in the same flower. The filaments incline themselves towards the centre of the flower, bringing the anthers into contact with the stigma there situated and pressing the pollen issuing from their loculi on to the receptive tissue. In some plants belonging to this category the displacement of the stamens, which is like the motion of the hands of a clock, is preceded by an elongation of the filaments, and in this respect the plants in question form a transition from those previously described, in the flowers of which autogamy is due to the growth of the filaments. As instances of these transitional forms may be mentioned *Azalea procumbens*, *Draba aizoides*, *Haplophyllum Bieberstеinii*, the numerous Saxifrages comprised in the groups of Aizoonia and Tridactylites, and more particularly many Alsineæ and other Caryophyllaceæ. The Saxifrages exhibit a number of individual peculiarities into which we cannot enter in any detail. We must content ourselves with describing two species as representatives of the two groups above referred to, and will select for the purpose *Saxifraga Burseriana*, a plant which grows in the eastern Dolomites, and flowers in early spring, and *Saxifraga controversa* of the group Tridactylites. The flowers of *Saxifraga Burseriana* are protogynous, and the two spreading stigmas are already susceptible of pollination at the time when the petals are only just open, and the anthers are still closed and held near the bottom of the flower on quite short filaments. During this first period of flowering the blossom is adapted to cross-fertilization. Soon afterwards the stamens in front of the sepals lengthen in definite succession, and the anthers,

which meanwhile have undergone dehiscence, are brought to the same level as the stigma. Although the horizontal distance between the stigma and anthers is very small, it is still sufficient to prevent the stigma from becoming coated with pollen from the anthers. Moreover, the stamens standing opposite the sepals incline outwards soon after, thus increasing perceptibly the distance between anthers and stigma. Synchronously with the outward inclination of these stamens there is an up-growth of those which stand in front of the petals, and here again the operation takes place according to a definite law of succession, and continues until the anthers are raised to the height of the stigmas. These anthers, like the others, do not adhere at first to the stigma, and it sometimes happens that the stigma remains unsupplied with pollen even on the sixth day of flowering if none is brought by insects. But, at last, on the seventh or eighth day some, if not all, the filaments move towards the centre of the flower, and the pollen-covered anthers are pressed against the stigma, which has not yet lost the power of receiving the pollen. Usually the five stamens opposite the sepals act in the same manner, and all the ten anthers then ultimately form a ring surrounding the stigma from which pollen may still be transferred by insects to other flowers. The flowers of *Saxifraga controversa* are likewise protogynous, and adapted to cross-fertilization in the first period of flowering. Of the ten stamens, the first to elongate are the five opposite the sepals; the anthers borne at their extremities ascend to the level of the stigma and during the process accomplish their dehiscence. For a short time anthers and stigmas are separated by a small interval of space, but soon afterwards the filaments incline a little towards the centre and deposit pollen upon the stigmas. The five stamens in question then slope away from the centre, and their empty and shrivelled anthers fall off. Meanwhile the five stamens opposite the petals have grown up to the level of the stigmas and offer a fresh supply of pollen for dispersion. But this pollen cannot be used for autogamy owing to the fact that the stigmas shrivel up after they receive the pollen of the first five stamens, and are no longer capable of playing a part in fertilization. The second supply of pollen can, therefore, only be appropriated to the fertilization of younger flowers through the instrumentality of insects. In other words, the five anthers in front of the sepals devote their pollen to autogamy, whilst the five opposite the petals devote theirs to cross-fertilization.

As in these Saxifrages so also in Alsineæ we find two whorls of stamens opposite the sepals and petals respectively, and a certain general resemblance unmistakably exists in the whole arrangement of the various parts of the flowers. The Alsineæ that we here have to deal with are protandrous, and as examples may be taken *Cerastium longirostre, Malachium aquaticum, Sagina saxatilis, Spergula arvensis,* and *Stellaria media.* Dehiscence takes place in the anthers opposite the sepals synchronously with the opening of the corolla, and the pollen exposed thereby is available for cross-fertilization. At that period the styles are still coherent, and the stigmatic tissue, which is composed of short transparent hairs, is inaccessible. Soon afterwards, however, the styles part asunder, and the stigmatic tissue assumes such a position as to ensure cross-fertilization in case insects bringing pollen from other

flowers should visit them in quest of honey. In a short time the stamens opposite the petals raise their anthers to the same height as the stigmatic tissue of the divergent styles; but the filiform filaments slope away from the axis, so that there is always some interval, however small it may be, between anthers and stigmas, and there is still no autogamy. It is not till the last moment, when the flowers begin to close, that the stamens opposite the petals incline towards the centre of the flower, and, laying their anthers upon the stigmatic tissue, cover it with a quantity of their still abundant store of pollen. In most of the Alsineæ, of which we are speaking, the anthers in front of the sepals also come into contact with the stigmas at the same moment, but in a few cases they project above the stigmas and petals, and their pollen is then not available for autogamy. It is remarkable that in the the latter, which may be represented by *Sagina saxatilis*, the characteristic fact of the pollen of the five stamens opposite the sepals being devoted to cross-fertilization, and that of the five stamens opposite the petals to autogamy, is exactly the reverse of the arrangement found to exist in the Saxifrages above described.

Next to this series of plants of which the Saxifrages of the Aizoonia and Tridactylites groups and the Alsineæ above-named are the chief representatives, comes another composed predominantly of Cruciferæ. They are for the most part annual species with small flowers, which are but little visited by insects, and the majority of their fruits must be looked upon as products of autogamy. *Cochlearia Groenlandica, Draba borealis, Draba verna, Clypeola Messanensis, Lobularia nummularia, Hutchinsia alpina, Schieverekia Podolica, Lepidium Draba, Alyssum calycinum*, are a few examples, and the selection shows incidentally that the range of the cruciferous plants in question extends from the extreme North to the latitude of the Sahara, and from high altitudes to the level of the deep-lying steppes; in fine, that this same process of autogamy recurs under the most diverse external conditions. All these Cruciferæ are protogynous, and have six stiff stamens, four long and two short. The anthers of the former are still closed when the flower opens, but are already on the same level as the stigma. Autogamy is, however, prevented immediately on the dehiscence of the anthers, owing to there being a little horizontal interval between them and the stigma. It is not till the flower is almost over that the erect filaments move sufficiently towards the middle of the flower to deposit the pollen upon the stigma. The pollen of the shorter stamens does not get transferred at all to the stigma in the same flower except in a few species. It is carried away by insects and used for cross-fertilization, whilst the pollen of the longer stamens mainly subserves the purpose of autogamy. *Lepidium Draba* exhibits a curious contrivance to prevent the four longer stamens from being touched by insects and despoiled of their pollen during the first part of the time that the flower is open. The stamens referred to bend outwards and hide themselves for a time behind the petals. The advantage of this movement is that in no circumstances can there be a deficiency of pollen for the ultimate process of autogamy. In *Hutchinsia alpina* usually only one of the four longer stamens approaches sufficiently near to the stigma to cover it with pollen, and after it has effected this object, it removes

itself again away from the axial position. All these movements are performed as a general rule with great rapidity. In *Alyssum calycinum* they take a few hours, in *Draba verna* the interval between morning and evening.

Some annual species of the Wood-sorrel genus—such as *Oxalis stricta*, for example—have five short and five long stamens in each flower. The anthers of the latter are of the same height as the stigmas, but begin by being at a little distance from them, so that at this period cross-fertilization may be effected by insects alighting upon the stigmas. Within the space of a few hours, however, the longer stamens incline towards the stigmas and deposit their pollen upon them. Here, again, the pollen of the five shorter stamens does not reach the stigma in the same flower, but is devoted to cross-fertilization. As in these annual species of Wood-sorrel, so also in the majority of species of St. John's-wort (*Hypericum*), the unequal length of the stamens, combined with the fact of the non-simultaneity of sexual maturity (*dichogamy*), is of advantage to the plant in that it ensures that autogamy shall take place just before the flower fades, whilst permitting at an earlier period cross-fertilization by the pollen of other flowers through the agency of insects. In *Hypericum perforatum*, which may be chosen as our example, the pistil is encompassed by a number of filiform filaments of unequal lengths, so arranged that the longest are in close proximity to the central pistil and the shortest near the periphery of the flower. The anthers do not liberate their pollen simultaneously, but one group does so after another. Dehiscence takes place first in the short stamens, next in those of median size, and last of all in the long ones. As soon as an anther opens, the filament bearing it inclines inwards, and thus one after another, the short, median, and long filaments stand up and approach the middle of the flower. It being only the anthers of the longest stamens that are on the same level as the stigmas, autogamy cannot occur till quite at the last, not long before the flower withers.

The widely-distributed Star of Bethlehem (*Ornithogalum umbellatum*) exhibits on the opening of the flower six stamens arranged in two whorls with three in each whorl. The stamens of the inner whorl are the longer, and their anthers dehisce a day sooner than the others. All six filaments look erect in the newly-opened flower, but are really sloped slightly outwards, with the result that the anthers are separated by an interval of about 3 mm. from the small stigma in the middle of the flower. So long as they maintain this position the pollen cannot be directly deposited upon the stigma, and the aim of the flower at this stage is to secure cross-fertilization through the intervention of honey-seeking insects. Towards the end of the flower's period of bloom both the long and the short stamens approach the centre, but only the anthers of the three shorter ones are applied to the stigma and besmear it with pollen; the other three do not come into contact with the stigma owing to their standing at a higher level. Thus the Star of Bethlehem differs from the cases previously described in that it devotes the pollen of the shorter stamens to autogamy and those of the longer stamens to heterogamy (cross-pollination). This is partly due to the circumstance that the anthers of the three longer stamens

are placed just in front of the approach to the nectaries of the ovary and in such a position are certain to be brushed by insects, whilst no honey is to be found behind the anthers of the three shorter stamens, and insects, therefore, make no attempt to enter past them. These anthers, consequently, retain their pollen, and when the flower is nearly over yield it up for the purpose of autogamy.

A curious contrivance is exhibited by *Aphyllanthes Monspeliensis*, a plant indigenous to Southern Europe. Like the Star of Bethlehem, it has three long and three short erect stamens in each flower, and the anthers are not at first in contact with the stigma. But before the final closing of the perianth all the stamens slope towards the stigma, which is subdivided into six lobes, three at the top and three lower down, so that the pollen of the three shorter stamens is deposited on the lower stigmatic lobes, and soon afterwards that of the three longer stamens is deposited on the three upper stigmatic lobes.

In many plants where all the stamens are of the same length, and where the anthers are already on the same level as the stigma at the time when the flower opens, the process of autogamy is essentially identical with that above described. The anthers are held by erect filaments at a little distance from the stigma, but later on, after various movements have been accomplished by the filaments, they adhere to the stigma and deposit their pollen upon it. This is the case, for instance, in *Paris quadrifolia*, in several species of *Scilla*, in *Chelidonium* and *Rœmeria*, in *Samolus Valerandi*, in *Androsace elongata*, *A. maxima* and *A. septentrionalis*, in *Lysimachia nemorum* and in *Swertia perennis* and *S. punctata*. It is not possible here to discuss all these plants individually, and only a few points in connection with them will be referred to. In the Herb Paris (*Paris quadrifolia*) the period during which each flower remains open is very long. The stiff stamens at first stand out radially, but later they describe an angle of 80° towards the middle of the flower, where they converge over the pistil and press their anthers upon the stigmas. In the plants of the order Primulaceæ—viz. *Samolus Valerandi*, *Androsace elongata*, *A. maxima*, and *A. septentrionalis*—the corolla is salver-shaped, and the short filaments, which are adnate to the tube of the corolla, only need to incline slightly towards the axis in order to transfer their pollen to the stigma in the same flower. The majority of these plants are protogynous; the flowers of *Swertia perennis* and *S. punctata* alone are markedly protandrous. There is, therefore, in the case of the latter no chance of cross-fertilization at the beginning of the period of flowering, the stigma being still closed. On the other hand, pollen is available for transport by insects to flowers that happen to be at a later stage of development. The next step is for the stigma to open and so dispose its two lobes that flies arriving with a supply of pollen from younger blossoms are obliged to effect cross-fertilization. To prevent restriction or frustration of this process of heterogamy, and also to ensure the preservation of some pollen for autogamy in the opposite case of an absence of insect-visitors, the five stamens bend outwards simultaneously with the opening of the stigma, exserting their anthers and hiding them under the stellately-expanded petals. If no insects come, and cross-fertilization is therefore

excluded, the filaments straighten themselves again and then move like the hands of a clock towards the middle of the flower, where they press their anthers, which still retain a little pollen, upon the stigma.

The stamens, which are instrumental in effecting autogamy by movements of inclination in the direction of the stigma, are straight at the commencement of the period of flowering in all the plants above enumerated. Sometimes they curve

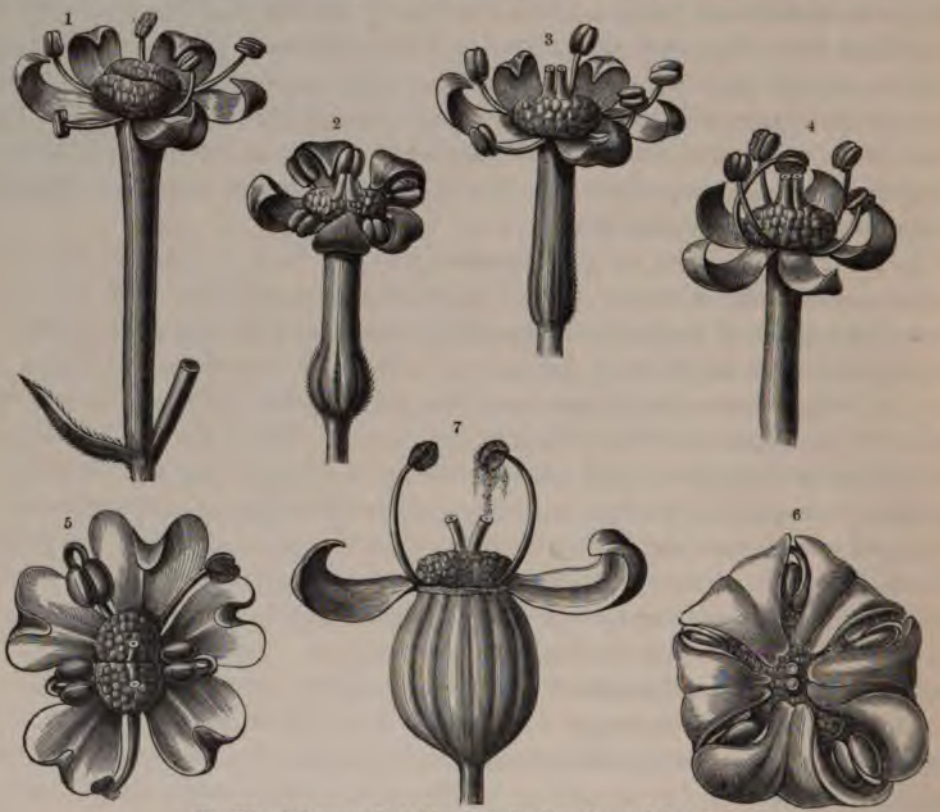

Fig. 296.—Autogamy effected by the inclination of curved stamens.

1 Pseudo-hermaphrodite male flowers of the Venus' Comb (*Scandix Pecten-Veneris*). 2, 3, 4 Successive positions assumed by the true hermaphrodite flowers of the Venus' Comb at first with a view to cross-fertilization, afterwards with a view to autogamy. 5, 6, 7 Successive positions assumed by the true hermaphrodite flowers of the Fool's Parsley (*Æthusa Cynapium*) at first with a view to cross-fertilization, afterwards with a view to autogamy. All the figures magnified.

outwards for a short time, but before the flower fades, and particularly at the moment of autogamy, they are invariably erect again.

There is, however, another group of plants to be considered in which the filaments are already inflexed in the bud, and continue so at the time when pollen from the anthers at their extremities is deposited upon the adjacent stigmas. The most important examples of plants exhibiting this autogamy by means of an inclination of inflexed filaments are afforded by several annual Umbellifers with protogynous flowers (*Æthusa Cynapium, Caucalis daucoides, Scandix Pecten-Veneris, Turgenia latifolia*, &c.). Two kinds of flowers are associated together in the umbels of the Venus' Comb (*Scandix Pecten-Veneris*; see fig. 296 [1, 2, 3, 4]),

namely, pseudo-hermaphrodite (*cf.* p. 294) male flowers (fig. 296 [1]) and true hermaphrodite flowers (figs. 296 [2, 3, 4]). The latter open earlier than the former, which, indeed, never come into play until the hermaphrodite flowers have cast both stamens and petals. Directly the petals open in the hermaphrodite flowers a finely-granulated honey-secreting disc and two short styles are revealed in the middle of the flower. The stigmas at the extremities of the styles are already mature, but the stamens are incurved like hooks and have their anthers still closed (fig. 296 [2]). The day after, also, when the petals have opened further back and

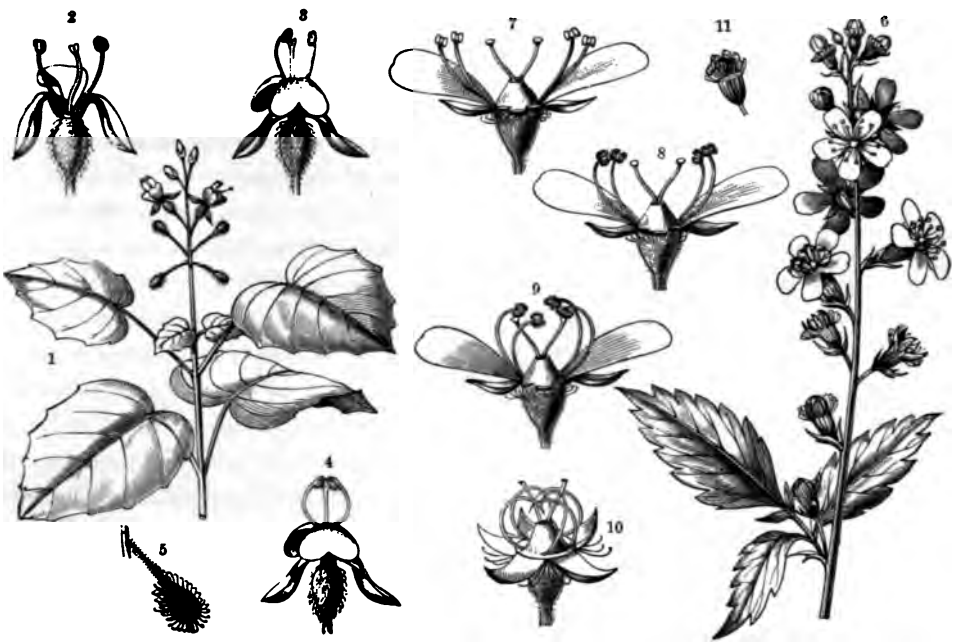

Fig. 297.—Autogamy effected by inclination of curved stamens.

[1] *Circæa alpina*. [2] A newly-opened flower of *Circæa alpina* with the front petal removed. [3, 4] The same flower at a later stage of development. [5] Fruit of *Circæa alpina*. [6] *Agrimonia Eupatoria*. [7, 8, 9, 10] Successive phases of a flower of *Agrimonia Eupatoria*, which is at first adapted to heterogamy (cross-pollination) and subsequently to autogamy. [11] Young fruit of *Agrimonia Eupatoria*. [1, 6, 11] natural size; the rest of the figures magnified.

the filaments have straightened out (fig. 296 [3]), the anthers surrounding the stigma in a circle are still closed, so that pollination can only take place at this period in the event of insects bringing pollen from other flowers. The anthers and filaments have, however, now entered upon an active phase. The curved stamens bend successively at short intervals, one after the other (after one has started, the next to follow is the stamen next but one to the left, and so on till all have done) towards the centre of the flower, bringing their anthers, which have meanwhile undergone dehiscence and are covered with pollen, into contact with the stigmas precisely in the manner shown in fig. 296 [4]. Each stamen only stays a short time in this position, and then executes a backward movement and makes way for the next in order. When all the stamens have accomplished these evolutions, they as well as the petals become detached and fall to the ground. The secretion of honey

on the rough surface of the pad of tissue in the middle of the flower ceases, the pollinated stigmas turn brown, and the period of bloom for that particular flower comes to an end. The imperfect staminiferous flowers do not unfold until all the hermaphrodite flowers are over, a fact which can only be interpreted as indicating that their pollen is to be devoted to the fertilization of protogynous hermaphrodite flowers of other individuals which are still in the first stage of flowering. Fool's Parsley (*Æthusa Cynapium*, see figs. 296 [5, 6, 7]) differs from the Venus' Comb and the other annual Umbellifers above referred to in that all the flowers of an umbel are hermaphrodite, and that the filaments, which in the bud are tucked in like springs (fig. 296 [5]), not only straighten out when the flower opens, but elongate, and thus raise the anthers to a higher level than the stigma. Also in Fool's Parsley, as has been mentioned before, the anthers are not laid right against the stigmas, but remain a little higher, and let their pollen fall upon them from above (see fig. 296 [7]). This at least is what I saw in the case of the common Fool's Parsley or *Æthusa Cynapium*; the small *Æthusa segetalis*, on the other hand, according to my observation, much more frequently brings its anthers into contact with the stigmas in the same manner as the Venus' Comb (see fig. 296 [4]).

Autogamy of the same type as that described in the above instances of annual Umbelliferæ also takes place in many small-flowered Bed-straws (e.g. *Galium infestum*, *G. Mollugo*, *G. tricorne*), in the Dodder (*Cuscuta*), in the Alpine Enchanter's Nightshade (*Circæa alpina*), and in Agrimony (*Agrimonia Eupatoria*). Of the Enchanter's Nightshade (see figs. 297 [1, 2, 3, 4]), it is only needful to note that the number of stamens is limited to two, and that sometimes one anther alone is laid upon the stigma (297 [3]), but not infrequently both subserve the purpose of autogamy in that manner (297 [4]). In the latter case the stigma looks as if it were grasped by the two limbs of a pair of tongs. The flowers of Agrimony have from 12 to 20 stamens, and are protogynous. The anther-filaments are very slightly incurved, each corresponding to about a sixth part of the circumference of a circle (fig. 297 [7]), but as soon as dehiscence takes place the filaments bend one after another towards the centre of the flower (see fig. 297 [8]) until they are in the form of semicircles, and some of the anthers covered with pollen come into direct contact with the stigmas, which are still in a receptive condition (fig. 297 [9]). Soon after the stigmas have thus been furnished with pollen the anthers drop off the filaments, and the latter coil up still more as is shown in fig. 297 [10].

Several species of Stonecrop (e.g. *Sedum annuum*, *S. atratum*, *S. dasyphyllum*), and some House-leeks (e.g. *Sempervivum montanum*, *S. Ruthenicum*) have two kinds of stamens in each flower, namely, those inserted in front of the sepals and those inserted opposite the petals. The anthers of the former are the first to open, and as they are quite close to the stigmas only a slight inclination of the curved filament is necessary to bring about autogamy. After a deposition of pollen upon the stigmas has already taken place, the filaments opposite the petals also curve over inwards, and the anthers, which meantime have undergone dehiscence, are held right over the stigmas. But, seeing that the latter are by this time withered

and have no further need of pollen, we are bound to infer that this fresh supply is offered for the purpose of effecting by insects' aid the fertilization of other flowers in which there is as yet no available pollen although the stigmas are accessible and mature. Opuntias and all the numerous species of the Rose genus (*Rosa*) behave in a similar manner. In them also some of the anthers devote their pollen to autogamy, whilst the others devote theirs to cross-fertilization. The filiform filaments are curved and of unequal lengths. The anthers borne by the innermost whorl of filaments open first, but their pollen is of no use for autogamy, notwithstanding the proximity of the stigmas, because the anthers are lower than the stigmas and do not spontaneously come into contact with them. Only the filaments of the outermost whorl are of the right length, and these alone curve over and lean towards the middle of the flower until their anthers rest immediately upon the stigmas. As, however, these anthers are the last to dehisce, autogamy does not ensue till the very last moment of flowering; for the whole of the time up till now the flower is adapted to cross-fertilization only.

In a number of Ranunculaceæ, such as *Anemone Hepatica*, *A. Transsylvanica*, *Ranunculus alpestris*, *R. acer*, and *R. montanus*, the structure of the flowers resembles to a certain extent that of Roses. A group of pistils with short styles and almost sessile stigmas rises up in the middle of the flower, and is surrounded by a large number of stamens which are arranged in several whorls and are in their turn encompassed by the petaloid sepals. The flowers are protogynous, and at the commencement of their period of bloom can only undergo cross-fertilization through the agency of insects. At a subsequent stage also after the dehiscence of the anthers of the outer whorl and the exposure of their adhesive pollen, the flowers are still adapted to heterogamy; for the distance of these anthers from the stigmas is comparatively great, and insects always alight on the group of carpels in the centre and make their way from them over the anthers to the circumference, whence they again take flight in order to visit another flower. But by degrees the stamens of the inner whorl also mature; the filaments, which hitherto have been very short, grow considerably and curve inwards, laying upon the stigmas their anthers which have meanwhile burst open. The sepals of these Ranunculaceæ close up when it begins to get dark, and the flowers assume a nodding position owing to a slight inflection of their pedicels. It might be supposed that these movements also are accessory to autogamy, and, as a matter of fact, in many other Ranunculaceæ, which will be the subject of discussion later on, such co-operation does occur; but, in the Anemones and Ranunculuses above referred to, no supplementary action of the kind is necessary, and the closing and nodding of the flowers in wet weather and during the night are resorted to merely with the object of protecting the pollen from moisture.

To this long list of plants with protogynous flowers must now be added a few protandrous species from the genera *Gypsophila*, *Saxifraga*, and *Cuphea*. The flower of *Gypsophila repens* contains ten stamens, of which five are inserted in front of the sepals and five in front of the petals. In the bud they are all tucked in like

hooks; in the open flower they are straight and slope outwards. Contact with the central stigmas, which meanwhile have become mature, is impossible so long as the stamens maintain the latter position; but shortly before the flower fades, the stamens become inflexed, and their anthers are thus brought against the stigmas. The Saxifrages also have two circles of stamens in each flower. In the species of the sub-genus Cymbalaria (*Saxifraga Cymbalaria, S. Huetiana,* &c.), the first to straighten out are those standing opposite the sepals. Their anthers open and display their pollen at a time when the adjacent stigmas are closed together, and are not as yet capable of taking up pollen. This supply of pollen is not therefore used for autogamy, but is obviously available for crossing with other flowers. After exposing their pollen one after another in definite order for a couple of days, these stamens incline outwards and let their anthers fall. The styles, now, for the first time, move asunder, and their stigmas become capable of receiving pollen. As the anthers of the stamens opposite the sepals have dropped off, and those of the stamens opposite the petals are still closed, the stigmas are only liable at this stage in the development of the flower to be dusted with pollen from other flowers or other plants. Eventually signs of vitality are also exhibited by the stamens opposite the petals. They become strongly inflexed, their anthers dehisce, and, the stigmas being still receptive, the period of the flower's duration is brought to a close by the anthers being pressed against the stigmatic surface and effecting autogamy. The same sort of thing is observed in the case of the protandrous flowers of several species of the genus *Cuphea*, as, for instance, in *Cuphea eminens*. These flowers, of which mention has already been made on p. 235 (figured on p. 237), face sideways and contain eleven stamens of varying length whose anthers are disposed in two irregular rows above the expanded calyx-tube. The style is short at the commencement of flowering, and is concealed, together with the immature stigma, underneath the anthers. Dehiscence occurs on the upper faces of the anthers which are turned away from the style, and the pollen issuing from the sutures is fated by its position to be rubbed off by honey-sucking insects, and to be eventually used for cross-fertilization. Two days later the style, which has in the meantime increased in length some 11 mm., projects above the stamens, bringing the stigma into the line of entrance to the honey (fig. 262 [2], p. 237). Should insects now visit the flower, bringing with them foreign pollen, cross-fertilization is certain to ensue. But, in the event of an absence of insects, the longest stamen bends up to the stigma and presses that face of the anther which is coated with pollen against the stigma.

The degree of inflection of the filaments in the cases hitherto described scarcely corresponds to the third of the circumference of a circle, and is but seldom actually spiral. But that more pronounced movements of inflection do occur for the purpose of effecting autogamy, is shown by the case of *Nicandra*, a plant belonging to the Solanaceæ, and that of *Calandrinia compressa*, belonging to the order Portulaceæ. In *Nicandra* the long filaments bend down to the extent of at least a semicircle to reach the stigma in the event of a failure of pollen from extraneous sources, and in the ephemeral flowers of *Calandrinia compressa*, the filiform filaments curve

gently away from the velvety stigma at 9 A.M., *i.e.* shortly after the expansion of the petals, whilst three or fours hours later, when the petals close up again, they undergo spiral inflection from right to left and lay their anthers upon the stigmas.

The cases in which the stigmas are the agents in the operation of transfer to themselves of pollen from the anthers of the same flower may be classed in two divisions, (1) those in which a direct contact between the stigma and the anthers is effected by some definite bending or other movement of particular parts of the pistil; and (2) those in which the pollen is first deposited by the anthers and stored in some part of the flower other than the stigma; ultimately the stigmatic tissue is brought in contact with it in the same manner as in (1), *i.e.* by some movement on the part of the pistil.

The cases comprised in the first division fall naturally into four groups.

To the first group belong all those in which autogamy is produced by *contraction* of the style. The Cactiform plants of the Mexican plateaux, in particular, various species of the genera *Cereus*, *Echinopsis*, and *Mammillaria*, exhibit in their flowers a number of filiform stamens, arranged in a close spiral around the passage leading to the honey secreted on the floral receptacle. In the midst of this thicket of stamens stands a long style which terminates in a stellate stigma. The anthers are already covered with pollen when the petals unfold, but the stigma, which projects considerably beyond the anthers, is still closed, its fleshy lobes being coherent and forming a kind of club, so that there can be no possibility of its being dusted with pollen. Thus the flowers are markedly protandrous, and the pollen liberated during the first part of their period of bloom can only be used for cross-fertilization. The next step is the opening of the stigma and spreading out of its lobes into a star in front of the entrance to the nectary. Insects now alighting are obliged to brush against the stigma before they can get at the nectar, and in so doing they deposit a portion of the store of foreign pollen with which they are laden upon the stigma and initiate a process of cross-fertilization. This stage may last a few hours only, or several days, or over a week, according to the species. When the term of the flower's duration is nearly reached the style contracts in length, and the stigma, which has hitherto been above the anthers, is drawn into the midst of them, so that it cannot fail to get covered with the pollen, of which there still remains a quantity clinging to the anthers. In *Cereus dasyacanthus* the stigma soon after the opening of the flower projects 1 cm. beyond the anthers. The length of the style bearing the stigma is at that time 20 cm. When the flower is nearly over, the style is only 16·5 cm. long, and the stigma is therefore drawn in through a space of 3·5 cm. and no longer surmounts the stamens, but, on the contrary, is 2·5 cm. lower than the anthers of the longest stamens.

The second group includes all cases where autogamy is brought about by an *elongation* of the ovary or the style. *Epimedium alpinum*, a native of the warm valleys of the Southern Alps, has four sepals arranged crosswise and beneath these —the flowers being partially inverted as shown in figs. 298[1, 2, 3]—four petals fashioned like little slippers and containing an abundance of honey in their blunt

saccate interiors. The ovary is spindle-shaped, and bears at the end of a short style a stigma covered with little papillæ. The stamens, four in number, rest with their dorsal surfaces in contact with the ovary; their anthers face outwards, are lanceolate in shape, and each carries on its apex a small foliaceous scale like the point of a spear (see fig. 298 [4]). The flowers are protogynous, or, in other words, the papillose stigma, which is hemmed in by the four scales just referred to, is already mature at a time when the anthers are still closed (fig. 298 [1]). At this stage the stigma may be dusted with pollen from other flowers. The next step is the dehiscence of the bilocular anthers, which takes place in a very peculiar manner. The wall of each anther-half which faces outwards becomes detached, and is lifted up in the form of a flap with the whole of the pollen of the corresponding cavity sticking to its inner surface. The two flaps then shrivel and roll up, with the originally internal surface outside, until the only point of attachment is just below the pointed scale at the apex of the anther; the free flaps arch over this foliaceous anther tip (fig. 298 [5]), and also over the stigma, which is close to the scale (fig. 298 [2]). The process is simultaneous in all four anthers, the result being that the stigma is roofed over by a vault composed of eight curved flaps, and as the exposed surfaces of the latter are thickly coated with pollen, the whole arch presents externally a continuous covering of that material (see fig. 298 [2]). Should insects now visit the flower to obtain the honey stored in the slipper-shaped petals they must brush past this pollen-covered vault; nor can they fail to be besmeared at the very spot where at a previous stage in the flower's development they would have had to brush against the stigma. This condition of affairs lasts usually for two days. In the meantime changes affecting the pistil are taking place which, notwithstanding their inconspicuous nature, are of the greatest importance in relation to the eventual accomplishment of autogamy. If the stigma is not dusted by insects with foreign pollen at the first expansion of the flower the pistil now elongates sufficiently to raise the stigma into the vaulted cavity just described; and as the flaps composing the vault curl up still more (fig. 298 [6]) as the flower approaches its end, the stigma must inevitably come into contact with the pollen adherent to them (cf. fig. 298 [3]).

A similar process is observed to take place in several Cruciferæ, of which the Charlock (*Sinapis arvensis*) is a typical instance. The flowers of this plant are protogynous. The bud opens early in the morning, revealing still closed anthers with their faces turned inwards (*introrse*), whilst the stigma is already mature and projecting somewhat above the anthers. At this stage of development no pollen except what is brought by insects can be deposited on the stigma. A day later the flower presents quite a different appearance. The four longer stamens have stretched and curved a little away from the axis, and the anthers are lifted above the stigma. By a rapidly executed twisting of the filaments the anthers have been turned round so as to face outwards, and extrorse sutural dehiscence has meantime taken place. The stigma is completely withdrawn from observation, and is also safe from any possibility of being dusted with pollen, for the anthers in the same flower have turned away their pollen-coated faces, nor is it possible for any extraneous pollen

that may happen to be brought by insects to be transferred to the stigma, owing to the anthers forming a hood over it. At this stage every other object is subordinated to the dispersion, through the agency of insects, of the pollen exposed by the flower. After the interval of another day the observer finds a third aspect of the flower presented to him. The filaments have straightened themselves out, and so brought the anthers nearer to the stigma; the coating of pollen has spread all over the anthers,

Fig. 298.—Autogamy brought about by elongation of the pistil.

[1, 2, 3] Flower of *Epimedium alpinum* at successive stages of development, showing primary adaptation to cross-fertilization and subsequent adaptation to self-fertilization. [4] Front view of a closed anther. [5] Side view of the same. The front (right-hand) wall of each of the two loculi has become detached and been raised up as a flap or valve. [6] The same anther; the flap has curled up more tightly and now forms a sort of cowl arching over the spear-like apex. [1, 2, 3] × 10; [4, 5, 6] × 25.

and the ovary has undergone elongation, carrying the stigma into the midst of the dome of anthers, where it becomes thickly overlaid with pollen

Again, in the nodding flowers of *Atragene alpina*, and in these of *Clematis integrifolia*, which grows freely in the swampy meadows of the Hungarian plains, we find autogamy effected by means of an advance of the pistil into proximity to the anthers laden with pollen. Both plants are protogynous—the stigmas being mature for a short time before the anthers dehisce—and in both the newly-opened

flowers are adapted to cross-fertilization. The stamens lie one upon another like the tiles of a roof, and together form a short tube at the bottom of which are a number of closely-clustered carpels, whilst at the free edge of the tube the anthers expose their store of pollen. The first anthers to open are those pertaining to the outermost and longest stamens, the next belong to those of median length, and the last to the shortest, which are in the immediate vicinity of the carpels. The pollen of the outermost anthers serves mainly for cross-fertilization, and can hardly ever be used for autogamy on account of its position; but even in the case of the latest anthers belonging to the shortest stamens, no pollen could reach the stigmas were it not for the elongation of the carpels, which occurs during the last two days of the flower's duration. The anthers still contain pollen at this late period, and a quantity adheres, besides, to the silky hairs clothing their filaments, so that the slightly divergent stigmas get covered with an abundant supply of pollen as the carpels lengthen and push them up through the pollen-coated tube (see fig. 246 [3], p. 174).

The flowers of the Lady's Mantle (*Alchemilla vulgaris*) are likewise protogynous. When a flower opens, the anthers of the four short stamens are still closed, whilst the stigma is already mature, and is seen in the middle of the flower projecting through and slightly above a kind of diaphragm which is stretched across the floral interior and secretes honey. At this stage cross-fertilization alone is possible; but in the course of twenty-four hours the style grows in an oblique direction, until its extremity bearing the stigma strikes against one of the four anthers, which have meanwhile undergone transverse dehiscence; it thus receives a sprinkling of pollen (see fig. 226 [5], p. 125). The pollen of the three other anthers is still available for transference by flies to the stigmas of other flowers.

The above are a few instances of the methods in which autogamy is effected by elongation of the style or of the entire pistil. Taken generally this process must be classed among the rarer forms of the phenomenon, though it is surprising that it should be so considering the frequency of autogamy by means of the elongation of stamens. The accomplishment of autogamy through the *inclination* of a style otherwise straight is of even less usual occurrence. The most striking example of this process is afforded by the bilabiate flowers of the North American *Collinsonia Canadensis*. In the newly-opened blossom the long style stands midway between two exserted stamens which are almost as long as the style. Towards the end of the flower's period of blossom, the style begins to slope towards one of the stamens, moving like the hand of a clock through an angle of from 20° to 40° until its stigma comes against the pollen-covered anther borne by the stamen in question.

A much more common method of bringing about autogamy is for parts of the pistil—usually the style—to bend so as either to bring the stigmas into direct contact with the anthers belonging to the same flower, or to place them in such a position beneath the anthers as to ensure their catching any pollen that may fall out of the loculi. The direction of the style's inflection depends upon the form and mode of insertion of the flower, and more particularly on the position assumed by the anthers. The flowers of the Great Mullein (*Verbascum Thapsus*), of the Corn-

salad (*Valerianella Auricula, V. carinata*, &c.), and of the non-twining species of Honeysuckle (*Lonicera alpigena, L. nigra, L. Xylosteum*) are protogynous, and the style is so placed when the corolla opens that its stigma must of necessity be brushed by insects as they make their way to the receptacle. There is evidently at this stage no possibility of any but cross-fertilization. Later on, when the anthers open and expose their pollen, the stigma is taken quite out of the way, the style becoming bent downwards or to one side, so that the stigma cannot come into contact with anthers of the same flowers either spontaneously or through the agency of insects. Not till the flowering period is nearly over does the style return to its original position; when this happens, the stigma is raised by the straightening up of the style, and is pressed against the anthers, which are still coated with pollen. The flowers of the Martagon Lily (*Lilium Martagon*) are nodding, and have their

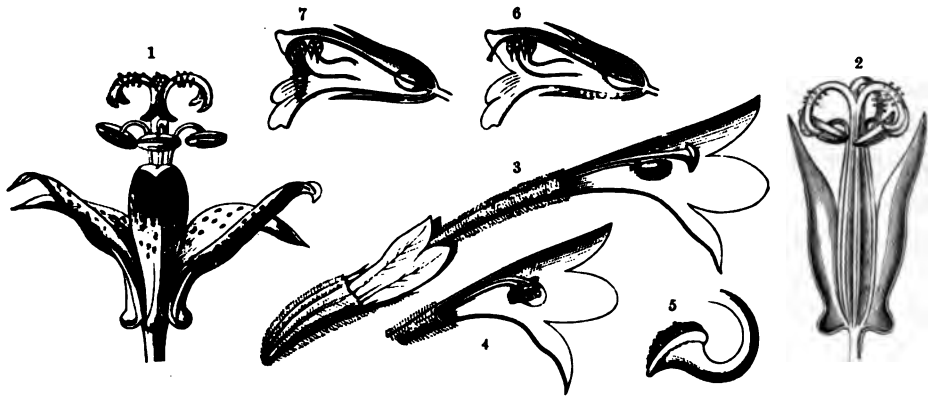

Fig. 299.—Autogamy effected by means of an inflection of the style.

[1] Flower of *Tricyrtes pilosa* in the first stage of its development. [2] The same in the last stage of development. [3] Flower of *Morina Persica* in the first stage of development. [4] The same in the last stage of development. [5] Stigma of *Morina* covered with pollen from anthers belonging to the same flower. [6] Flower of *Euphrasia minima* in the first stage of development. [7] The same in the last stage of development. All the figures slightly magnified. In figs. [2], [3], [4], [6] and [7] the front part of the flower is cut away

perianth-lobes strongly reflexed. In each petal there is a groove which is roofed over and closed in the middle by two coalescing rims, so that the honey stored in the groove can only be sucked out by insects at the two extremities where the groove is open. The flowers are protogynous, and, when they are newly open, the style is straight and holds its stigma in such a position that it is sure to be touched by insects sucking honey from the inner orifice of the groove. As the anthers are still closed at this stage, only foreign pollen can be affixed to the stigma. Subsequently dehiscence ensues, and the position of the anthers in front of the external orifice of the groove ensures their pollen being brushed off by insects trying to suck the honey at that end, whilst the stigma is left untouched by them. In this second stage of the flower's development the style begins to bend a little to one side, and, towards the end, the curvature increases to such an extent that the stigma comes into contact with one or sometimes two of the anthers, and dusts itself with pollen. Often enough, it is true, the stigma misses its mark, and in consequence autogamy is not so certain to occur in the Martagon Lily as in most of the other cases. It

must also be noted that the inflection of the style only takes place should the stigma have not previously been supplied with extraneous pollen. If there has been cross-pollination at the commencement of flowering the inflection either does not occur at all or is so trifling as to be of no significance.

The transference of pollen to the stigma by means of a bending down of the style is observed in various species of *Tricyrtes*, *Morina*, *Œnothera*, and *Epilobium*, in several Rhinanthaceæ, Caryophyllaceæ, and Ranunculaceæ, and in most of the Malvaceæ. The flowers of *Tricyrtes pilosa*, of which figures are given above, are protogynous. Each of the three styles is bent down, and has a bifurcated extremity, so that it looks not unlike a claw. The stigmatic tissue is situated at the end of the claw, and is brushed by insects on their alighting to suck honey from the saccate bases of the perianth-segments. The free extremities of the filaments curve down in semicircles, and the anthers are suspended under the claws of the style (fig. 299 [1]). At the time when the anthers have their pollen exposed they are so situated as to stand in the way of insects coming in quest of honey. Without the assistance of insects there could be no transference of pollen to the stigma so long as stigmas and anthers remained in the same relative positions, and the flower remained upright. But the chance of insects not visiting the flower is provided for by a downward bending of the claws of the style, which continues until the stigmatic tissue at their extremities comes into direct contact with the pollen-coated anthers (see fig. 299 [2]).

The process above described takes place in the course of a week in *Tricyrtes pilosa*, but in *Morina Persica*, one of the Dipsaceæ (see figs. 299 [3, 4, 5]), it is all accomplished within a few hours. The difference between the times at which stigmas and anthers respectively attain maturity in *Morina* is scarcely half an hour, but even this short interval suffices to render cross-fertilization possible during the first stage of flowering, whilst in the second stage autogamy obtains. All the species of the genus *Morina*—including *Morina Persica*, the type here selected for illustration—unfold their flowers at dusk. As soon as the corolla-limb expands the thick pulvinate stigma becomes visible in the middle of the flower just above the entrance to the honey. The receptive tissue is on the upper surface of the stigma. The two anthers are stationed behind the stigma, and when insects insert their probosces into the long honey-filled tube of the corolla they are certain to effect cross-fertilization, provided they have previously visited flowers at a somewhat later stage of development. In the case of other plants whose flowers open in the morning it would be scarcely likely that insects should alight immediately after the opening of the passage to the honey, but the flowers of *Morina* are adapted to crepuscular and nocturnal moths, which only have two or three hours of darkness in which to get the honey, and must, therefore, make great haste and employ the whole of the time if they are not to fail in their quest. As a matter of fact the moths in question leave their haunts within a quarter of an hour of the time when the flowers of *Morina* open, and one may be sure that wherever Sphingidæ and Noctuæ with probosces 3 or 4 centimetres in length abound, one or more will come flying to suck the honey as soon as the floral receptacle becomes acces-

sible. Thus, dichogamy, involving hardly half-an-hour's interval between the attainment of maturity in stigmas and anthers respectively, is sufficient to ensure cross-fertilization at the commencement of the period of bloom in each flower of this kind of night-flowering plant. A further adaptation with a view to heterogamy is shown in the position of the stigma in front of the anther in the first stage of floral development (see fig. 299 [3]). On the intrusion of insects—Sphingidæ, Noctuæ, &c.—into the interior of the flower the large stigma is the first object encountered, and next to it come the anthers, and there is therefore a possibility that even during the time that the anthers are open and have their pollen exposed cross-fertilization may take place through the agency of insects. If, however, no insects visit the flower the style bends down the very next morning in an open curve and lays the stigma flat upon the anthers (see fig. 299 [4]). The pollen readily adheres to the surface of the stigma, as may be seen by removing that organ after it has become appressed to the anthers, when a thick layer of pollen will be found sticking to it (fig. 299 [5]).

Inflections of the style in all respects similar to those exhibited in *Morina* occur in the flowers of numerous Rhinanthaceæ, *e.g.* in *Rhinanthus minor*, *Trixago apula*, *Melampyrum pratense*, *Euphrasia minima* (see figs. 299 [6] and 299 [7]). In these plants we find, in general, a repetition of the entire process above described, except for the circumstance that the pollen is not adhesive but mealy, and is not transferred to the receptive tissue by appression of the stigma to the anthers—it being sufficient to place the stigma under the anthers by means of an inflection of the style. The stamens in this case are of the sugar-tongs type (*cf.* p. 271). In the first and second stages of floral development the mealy pollen only falls out of the anthers on the occasions when the stiff filaments of the stamens are forced apart by insects. Should no insects visit the flower the pollen remains in the loculi. In the third stage of flowering the filaments become flaccid, as does also the portion of the corolla adjacent to them, and in consequence the anthers, which have hitherto been closely coherent, move a little apart from one another and let the pollen fall out. Meanwhile the style has bent down sufficiently to bring the viscid stigma under the front pair of anthers, so that a portion of the pollen is caught upon its glistening surface, with the result that autogamy is effected (see fig. 299 [7]). It is not uncommon for the inflection of the upper third of the style to be so strong as to amount to an involution, and the stigma is then pushed between the disuniting anthers and comes into contact with the hairs which clothe the anthers, and which are usually powdered all over with pollen.

Tricyrtes, *Morina*, and the Rhinanthaceæ just mentioned, are all protogynous, whilst on the other hand, the Evening-primrose, Willow-herb, Campion, and Mallow, in which autogamy likewise occurs in consequence of the style bending down to the anthers, are protandrous. When the petals of the Evening-primrose (*Œnothera biennis*, *Œ. muricata*, &c.), or of the large-flowered species of Willow-herb (*Epilobium hirsutum*, *E. angustifolium*, see fig. 300) expand, the four branches of the style, which bear the receptive tissue and constitute the stigmas, are closely

coherent, whilst a further condition, which would also render pollination impossible, consists in a lateral inclination or sharp inflection of the style which removes the stigma out of the way leading to the honey. The eight anthers then stand in front of the spots where honey is to be obtained, and liberate their pollen in turn. A little later—half an hour in Evening-primroses, and 24 hours in the large-flowered species of Willow-herb—the style straightens itself and takes up a central position in the flower, whilst its four branches open back and present themselves in the form of a cross in front of the entrance to the honey. The stigmas remain in this position for a short time, and there is no need to enter into more detail to make it evident that cross-pollination may now be effected by the humble-bees which come in search of honey and bring with them a store of pollen from younger flowers. Soon afterwards, the four stigmas bend or roll back, bringing their receptive tissue into contact with the pollen still adhering to the anthers (see fig. 300, the lower flowers). This act of autogamy is usually promoted also by the stamens becoming rather more erect and by an inflection of the stalk-like inferior ovary in a gentle curve towards the ground, the result of which is that the flowers nod, *i.e.* are half-inverted.

Fig. 300.—Autogamy in the flowers of the Willow-herb (*Epilobium angustifolium*).

Of the Ranunculaceæ, a few species of Love-in-a-mist (*Nigella*) exhibit the same kind of contrivance. The flowers are protandrous. The first event to take place after the expansion of the sepals is a bending of the stamens in regular sequence towards the periphery of the flower, whereby the open anthers are posted just above the nectaries full of honey. Insects coming in search of honey must inevitably rub against the anthers in that position and dust themselves with the pollen. After the stamens have all accomplished these movements, the styles, which have hitherto stood stiffly erect and stationary, enter upon an active phase and bend outwards until their terminally-placed stigmatic tissue, which, meantime, has become mature, rests over the nectaries. In this position the stigmas are certain to

be dusted with pollen from younger flowers brought by the insects which come in search of honey. The process of outward inflection of the styles is, however, not yet completed, but continues until the stigmas strike against the anthers and take from them some of the pollen still clinging to their surfaces.

There are also some caryophyllaceous plants (*Lychnis alpina, Alsine Gerardi, Cerastium arvense, C. lanatum, Stellaria graminea, S. Holostea*) which exhibit, just before the flowers wither, inflections enabling the stigmas to possess themselves of the pollen of the anthers in the same flower. The flowers are incompletely protandrous. First of all, the stamens inserted opposite the sepals come to maturity while the stigmas in the same flower are still incapable of receiving pollen. The pollen offered by these stamens can therefore only be used for cross-fertilization. The next day their filaments bend as far as possible towards the periphery of the flower, and many of them lose their anthers. Meanwhile, the stamens standing opposite the petals grow longer and their anthers dehisce so that their pollen also is rendered available for transference by insects. A day later these stamens bend slightly towards the periphery of the flower, but they never lose their anthers, which continue to offer their pollen till the flower withers. On the fourth day the styles, which have hitherto stood in the middle of the flower, separate from one another, curve over backwards, and, in some species, become twisted into spirals. The stigmas are thus brought into contact with the anthers last mentioned and take up some of the pollen with which they are covered.

In the Caryophyllaceæ whose names are given above the inflections of stamens and styles take four or five days; in Mallows (*Malva borealis, M. rotundifolia*, &c.) the same processes are completed within 48 hours, and in *Hibiscus Trionum*, and in *Abutilon Avicennæ* within from three to eight hours. When the flower of a Mallow is just open a sheaf of filaments bearing round anthers covered with pollen may be seen enveloping and roofing over the styles. Soon after, however, the filaments of which the sheaf is composed become reflexed and a bundle of styles is then seen occupying the place previously filled by the stamens. The stigmatic tissue has matured in the meantime. The parts of the flower do not remain long in this position, which is obviously adapted to cross-fertilization by insect agency; the styles coil into the shape of an S and at the same time bend down until the fringe of papillæ constituting the stigmatic tissue comes into contact with the pollen of the anthers which have shortly before been lowered by the inflection of their filaments. In *Abutilon Avicennæ*, which grows abundantly in Hungary on the banks of the river Theiss, the sheaf of filaments does not at any time form a roof over the style, but, from the moment the petals unclose, five slender styles, terminating in spherical red stigmas with velvety surfaces, may be seen projecting above the anthers. Insects alighting upon the velvety stigmas or brushing against them may cause heterogamy at this period; but a couple of hours later the styles curve down, and the stigmas are appressed to the anthers which are covered with an abundant store of pollen. Other Malvaceæ, *e.g. Anoda hastata*, behave in an opposite manner as regards the inflection of the style. In the buds of these plants

both filaments and styles are sharply bent over towards the floral receptacle. After the expansion of the petals, the filaments straighten out and together constitute a sheaf of filiform stalks, each of which bears an anther covered with pollen. A little later it is the turn of the styles to become erect. They perform the same movements as have previously been executed by the stamens, and push themselves into the midst of the stamens. By these evolutions the stigmas of the longer styles are placed a little above the anthers, whilst those of the shorter styles are brought into direct contact with the anthers, and take from them some of the pollen of which there is always a certain quantity left so that autogamy invariably ensues.

The method of self-fertilization adopted by the Sun-dew (*Drosera*) is somewhat like that just described. In *Drosera* the spherical ovary supports three styles, each of which divides into two spatulate lobes bearing the stigmatic tissue on their upper surfaces. The open flower is cup-shaped, and in it these lobes may be seen spread out horizontally like the spokes of a wheel (see fig. 279[10], p. 279). The stamens, on the other hand, are erect, and cross the lobes at right angles, holding the anthers above the stigmatic tissue. As soon as the petals begin to close, the stigmatic lobes rise up until they touch the anthers.

In several Labiates and Lentibulariaceæ autogamy is dependent on inflections, not of the style but of the stigma. This occurs, for instance, in the Hemp-Nettle (*Galeopsis ochroleuca, G. Tetrahit*, &c.), where the flowers are protandrous, and so adapted as to ensure cross-fertilization in the event of insects visting them. Towards the end of the flower's period of bloom the stigmatic extremity of the lower arm of the style bends downwards and backwards until it touches the pollen-coated anthers of the longer stamens; in the case of many species of the Wound-wort genus (*Stachys palustris, S. sylvatica*, &c.) both stigmatic arms bend down a short time before the flower fades and take the pollen from the anthers. The flowers of the Butterwort (*Pinguicula*; already described at vol. i. p. 142), which face sideways, contain two ascending stamens terminating in patelliform anthers, and above them an egg-shaped ovary surmounted by a large lobate sessile stigma. The lower border of the stigma which bears the receptive tissue hangs down like a curtain over the anthers. Insects, in the act of inserting their probosces into the honey-containing spur, brush first against this stigmatic border, and next against the anthers behind it. Thus they dust the stigma with the pollen they bring from other flowers, and the next moment load themselves with a fresh store which they carry off to yet other plants. The conditions are, in the first instance, adapted to cross-fertilization, and very frequently this form of reproduction occurs in the plants in question; but if no insects visit a flower the pendent stigmatic border rolls up sufficiently to bring the receptive tissue against the anthers. There being still plenty of pollen on the anthers, autogamy is then certain to ensue. The same phenomena may be observed in flowers of the Bladder-wort (*Utricularia*), and probably in those of the majority of Lentibulariaceæ.

A comparatively rare method of autogamy is for both filaments and style to coil up in spirals and become entangled just before the flower fades, the stigmas being

brought in the process of involution into contact with the pollen of one or more anthers. Most of the plants which exhibit this curious phenomenon have the common property of being ephemeral, but they belong to most different families. In a number of Commelynaceæ—*Commelyna cœlestis*, for example (see fig. 301)—the stigma is situated in front of and lower than the anthers when the flower, which faces sideways, is quite newly open (fig. 301[1]). Honey is secreted on curious palmately-lobed nectaries, and if in this first period of the flower's development insects come in quest of the honey they make use of the anthers to alight on, and in so doing besmear themselves with the pollen, which is already emerging through the lateral sutures of dehiscence of the anthers. Soon afterwards the stamens become spirally coiled, and the style, which meanwhile has grown to the same length as the stamens, curves in such a manner as to bring the stigma to a somewhat higher position than it previously occupied, and to make it the most con-

Fig. 301.—Autogamy by means of spiral twistings of stamens and style.

[1] Flower of *Commelyna coelestis* in its first stage. [2] In its second stage. [3] In its third stage of development. All in longitudinal section and slightly magnified.

venient place for insects to settle upon (fig. 301[2]). The arrival of insects which have visited younger flowers is at this stage sure to be accompanied by cross-fertilization. This state of affairs, however, only lasts a very short time. The style then winds itself into a spiral, and becomes entangled with the coiled stamens, with the inevitable result that the stigma comes into contact with one or other of the anthers, and gets covered with pollen (fig. 301[3]). The whole process occurs in almost exactly the same manner in the flowers of *Allionia violacea*, of *Mirabilis Jalapa*, and several other Nyctaginaceæ. As regards *Allionia violacea*, it is only necessary to observe that the flowers are protogynous, that the stigma is higher than the anthers at 6 a.m., when the flower opens, that a few hours later the anthers are raised to a higher level than the stigma in consequence of certain peculiar movements of the style and stamens, and that by 10 o'clock the involution of the filaments resulting in autogamy has already begun. In the newly-opened flower of the Marvel of Peru (*Mirabilis Jalapa*) the dot-like stigma is situated in front of the anthers, and in the event of insects coming in search of honey, it is first the papillæ of the stigma and afterwards the anthers that are touched by the intruders. No raising and lowering of filaments or style takes place in this case,

but a process of involution like that exhibited in *Allionia* ensues, and as soon as autogamy has been initiated the limb of the perianth folds up, turns pulpy, and then forms a kind of stopper above the knot of twisted filaments and style. The flowers of the Purslane (*Portulaca oleracea*) differ from those of *Commelyna*, *Allionia*, and *Mirabilis* in having five stigmas which are like delicate feathers in form, and are spread out in a star in the middle of the erect flower-cup. The stamens project obliquely from the receptacle, and are arranged in a circle round the stigma; but when the flower opens first, there are little spaces between anthers and stigmas, and this prevents a spontaneous transference of pollen to the stigmas. After the lapse of a few hours the petals, which in the sunshine are expanded in the form of a cup, draw together, and the flower begins to close up; all the five feathery stigmas bend over to the same side and gradually coil up into spirals. The thread-like stamens also undergo inflection, at first into semicircles, and subsequently into spirals, and the pollen-coated anthers are in consequence pressed against the stigmas. At this period, in the Purslane as in the Marvel of Peru and other plants whose flowers are ephemeral, the petals may be seen in a pulpy condition covering over the knot of tangled filaments.

As has been said before, this form of autogamy occurs chiefly in flowers which last only a single day. Where the whole period during which the flower is open is but a few hours the movements in question may all be followed by the observer. In the few species, which resemble the foregoing in respect of autogamy, but differ from them in that their flowers remain open two or three days, or even longer, these movements of inflection and torsion take place much more slowly. Thrifts (*Armeria alpina*, *A. vulgaris*, &c.) display in the middle of each of their cup-shaped flowers five stigmas disposed in the same manner as those of Purslane-flowers. The stigmas in this case, however, are not feathery, but in the form of slender cylinders covered with short, closely-packed papillæ, which give them a velvety appearance. The stamens are adnate to the short corolla-tube, and rise up in front of the petals holding their anthers between the rays of the stigma. Notwithstanding the proximity of the anthers to the stigmas, neither in the first nor in the second stage of the flower's development is any pollen transferred, without extraneous aid, to the receptive stigmatic tissue. At first the stamens are so placed as to have their anthers brushed by insects visiting the flower, whilst the five stigmas are still erect. A little later the anthers and stigmas change places as in so many other cases; the stamens stand up and bring the anthers together nearer the middle of the flower, whilst the stigmas diverge from one another, and place themselves close to the way leading to the honey. Attention has been so often directed to the connection between an interchange of position of this kind and the accomplishment of cross-fertilization that it is needless to repeat the facts of the case. Supposing, however, that insects do not visit the flower, and that, in consequence, heterogamy fails, the styles wind themselves up spirally, and move at the same time towards the middle of the flower, where they become entangled with the filaments, which have likewise undergone spiral torsion. In these circum-

stances, the velvety stigmas cannot fail to receive the pollen that still adheres to the anthers.

It appears from what has been said concerning autogamy that in a large number of plants the pollen developed in the anthers, especially if it be of the adhesive variety, still occupies the recesses of the anthers, or sticks to the reflexed margins of the lobes after their dehiscence, at the time when the flower fades. Even after insects have brushed off a portion of the pollen and transported it to other flowers, there is still invariably an abundant supply for the purpose of autogamy, and it is only in rare cases that loculi, in which adhesive pollen has been matured, are completely emptied by the end of the flowering period. In some plants, however, the adhesive pollen is swept out or removed in some other way from the anthers by means of special contrivances as soon as it is mature, and is then deposited on some particular spot in the flower where it is exposed for dispersal. In the case of the pollen of Composites it is well-known that it is pushed out of the tube of connate anthers by the style, owing to the growth of the latter organ which is sheathed within the anther-tube, and that it appears at the top of the tube in the form of a lump capping the extremity of the style. In Bell-flowers (*Campanula*), the entire contents of the anthers are stored upon the surface of the style, and the same thing happens in the various species of the Rampion genus (*Phyteuma*) and in some small-flowered Gentians. The shrivelling of the anthers is in many plants the cause of their shedding a portion of their pollen, and it may then collect on capillary appendages of the ovary, in cup-shaped petals, or on some other part of the flower where it is stored up for future use. It must often happen, too, that when insects are in the act of taking the honey they push against the stamens, and that the pollen shaken out of the anthers by their impact adheres to particular parts of the corolla, calyx, or perianth. This pollen is just as available for fertilizing purposes as that which remains sticking to the anthers, and we meet with cases where the stigmas fetch the pollen developed in the same flower from its temporary resting-place, and so bring about autogamy. Contrivances for this purpose are not numerous, but the number of species in which this form of autogamy prevails is extremely large. The abstraction of pollen deposited on the outer surface of the stylar column or its arms by stigmatic tissue situated on the edges or the inner surface of these style-branches occurs in hundreds of Campanulas and thousands of Composites, and shall therefore be chosen as our first example of this type of process.

Two modes of operation may be distinguished: first, a crossing; and, secondly, a spiral revolution of the style-branches. The former process is observed particularly in the Asteroideæ (*Aster*, *Bellidiastrum*, *Erigeron*, *Solidago*), especially in the tubular flowers in the middle of the capitula of these plants; but it is also seen in many Composites possessing ligulate flowers only. In *Aster alpinus*, the species selected for illustration (see figs. 302 [1, 2, 3]), the stylar arms are short and thickish; their inner surfaces are smooth and flat, whilst their outer surfaces are a little arched, and towards the free extremities are furnished with papilla-like sweeping-hairs. The receptive stigmatic tissue is situated on the margins of the style-

branches below the sweeping-hairs, and may be recognized by the granulated appearance of its turgescent cells. The behaviour of the stylar branches from the commencement to the termination of a flower's bloom is shown in fig. 302[1], where the three tubular florets are in successive stages of development. Almost simultaneously with the opening of the tubular corolla the two style-branches are pushed up above the anther-tube, and the pollen is swept out of the tube by the hairs previously referred to. The style-branches at this period are in close contact, and the receptive tissue of the stigmas is not yet accessible (fig. 302[1], left-hand floret).

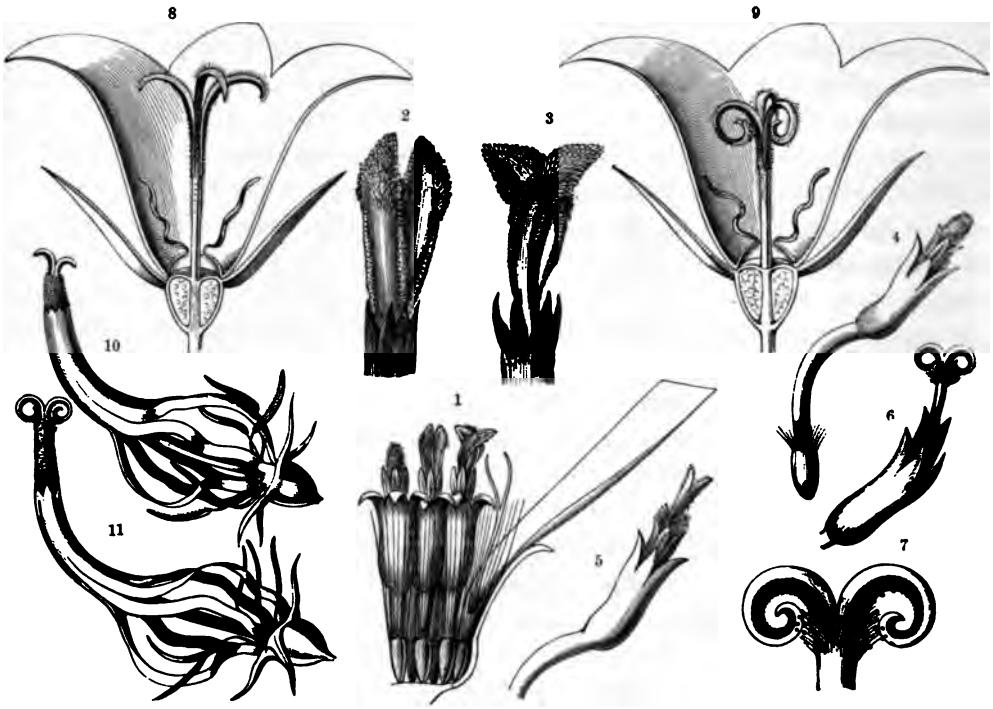

Fig. 302.—Autogamy by means of a crossing or a bending back of the style-branches.

[1] *Aster alpinus.* Portion of a capitulum, including a marginal female floret with ligulate corolla and three tubular florets of the disc. The latter are in the successive stages which lead to autogamy (left to right). [2] Style-branches of *Aster alpinus* which have just separated but still have some pollen clinging to their hairs. [3] The style-branches crossed so as to transfer the pollen from the collecting-hairs of the one to the stigmatic tissue of the other. [4], [5], [6] Florets from the centre of a capitulum of *Centaurea montana* in successive stages leading to autogamy. [7] The two style-branches rolled back sufficiently to bring the stigmatic tissue into contact with the pollen on the collecting-hairs. [8] *Campanula persicifolia*; longitudinal section through a newly-opened flower. [9] The same with the style-branches rolled back so as to bring the stigmatic tissue into contact with the pollen on the exterior surface of the stylar column. [10] Flower of *Phyteuma orbiculare* in process of transition from the first to the second stage of development. [11] The same flower in the last stage of development. [8], [9] natural size; the rest magnified.

Neither cross- nor self-fertilization of the flower in question can at present be effected, and the pollen is only exposed that it may be carried away by insects to fertilize other blossoms. The two style-branches are subsequently lifted still higher and move a little apart, with the result that the pollen clinging to their hairs, if not already removed by insects, is for the most part pushed off, falls down, and is appropriated to the purpose of geitonogamy (see p. 321). A small remnant of pollen is, however, invariably left hanging to the lower collecting-hairs, and this it

is which is devoted to autogamy (see fig. 302 [2]). The process of self-pollination is the last to take place. The two style-branches bend and cross one another, and in so doing bring the pollen adhering to the lower hairs of the one arm into immediate contact with the receptive tissue on the margin of the other arm. In this position the two style-branches resemble the beak of a cross-bill, as may be seen in fig. 302 [3]. The style-branches of those Composites whose capitula consist entirely of ligulate florets, are always much longer than those of the Asteroideæ; they are of thread-like appearance, and the lower parts of their external surfaces are beset with collecting-hairs. In one section of these Composites, including, for instance, *Crepis grandiflora*, *Hieracium umbellatum*, and *Leontodon hastile*, there is likewise, shortly before the flowers fade, a simultaneous inflection and spiral involution of the two branches of the style resulting in autogamy; it reminds one, even more forcibly than the case of Asteroideæ, of the action of a person when he crosses his arms.

The second kind of process, viz. the spiral re-volution or bending back of the style-branches, may be particularly well seen in the Groundsels—*Senecio Fuchsii* and *S. nemorensis*—and in Centaureas. We will select as an example *Centaurea montana* (see figs. 302 [4, 5, 6, 7]), which grows abundantly in the lower Alps. The styles are fashioned quite differently from those of the composite flowers to which reference has been made above. The stigmatic tissue is spread out over the inner surface of the style-branches, especially over the part near the free extremity, and the collecting-hairs are confined to a narrow zone underneath the point of bifurcation of the style. The pollen is swept out of the anther-tube (see fig. 302 [4]) in the same manner as in the other Composites, but in *Centaurea* the process of extrusion is accelerated by a sudden contraction of the irritable filaments of the stamens when they are touched by insects (*cf.* p. 252). After most of the extruded pollen has been removed by insects or scattered by the divergence of the style-branches (fig. 302 [5]), the receptive inner faces of the latter are so disposed as to ensure cross-pollination in the event of insects coming laden with pollen from other capitula. This state of affairs, however, only lasts a short time; the two style-branches soon roll back and bring the receptive tissue of their originally inner faces into contact with the pollen left upon the hairs, thus effecting autogamy (see figs. 302 [6] and 302 [7]).

Bell-flowers (*Campanula*) exhibit for the most part the same bending back of the style-branches, and the phenomenon has the same significance in them as in composite flowers, but the manner in which the pollen is transferred to the external surface of the style is somewhat different. Within the closed bud the long anthers are adjacent to the central column of the style, as in Compositæ, and form a kind of tube round it. These anthers open inwards, too, and deposit the whole of their pollen on the outside of the style, which is furnished with delicate transparent papillæ, and is in consequence well adapted to the retention of the pollen. The pollen is not, however, swept out of the tube of anthers, but the anthers, after depositing their pollen upon the stylar column, separate from one another and shrivel up, and only persist as shrunk and empty relics at the bottom of the flower (see fig. 302 [8]). The style-branches are by this time divergent, and occupy a posi-

tion in the mouth of the corolla, which necessitates contact between the receptive tissue at their tips and the bodies of the humble or hive bees, which find their way to the flower in search of honey. If these insect-visitors bring with them pollen from other flowers, cross-fertilization is inevitable. As they push lower down into the flower, the bees receive an additional load of pollen from the stylar column, the surface of which is coated with it, and this new store they may convey to other blossoms. When the time for the flower to fade is near at hand, the style-arms become revolute, and press the receptive tissue of their tips upon the stylar column, taking from it a coating of pollen, of which there is still a sufficient quantity clinging to the surface (see fig. 302 [9]). The large-flowered *Campanula persicifolia* has been selected as a type of these Bell-flowers. The style-arms in this species are from 1 cm. to 1·6 cm. long, and they coil into spirals of from 1½ to 2 involutions. In most of the other Bell-flowers (e.g. *C. barbata, C. carpatica, C. pyramidalis, C. Rapunculus, C. spicata*) the revolute style-branches have only from 1 to 1½ coils in each spiral, whilst in some few (e.g. *C. patula, C. rapunculoides*) there are rather more than 2 complete coils in each. The Rampion genus (*Phyteuma*), here exemplified by *Phyteuma orbiculare* (see figs. 302 [10] and 302 [11]), differs from the Bell-flowers, which are its nearest allies, in the circumstance that the deposition of pollen and retraction of the emptied anthers occurs at a time when the tips of the petals are still connate into a tube. For a short time the end of the stylar column may be seen covered with pollen projecting beyond the corolla, and in this position the two arms disunite and expose their stigmatic tips to pollination by insects (see fig. 302 [10]). If no insects visit the flower the style-branches roll back and bring their tips into contact with the pollen on the stylar column (see fig. 302 [11]). In all the species that have been examined (*Phyteuma confusum, P. hemisphæricum, P. Halleri, P. orbiculare, P. spicatum*) the style-branches are wound into from 1 to 2 complete coils. In the case of *Phyteuma Halleri* the further observation was made, that after the accomplishment of autogamy the transparent hairs on the stylar column and the pollen adherent to them rapidly dry up, whilst the branches of the style unroll again.

Of the Gentians, the little *Gentiana prostrata*, which grows on the mountains in the vicinity of the Brenner Pass in Tyrol, affords a striking example of the phenomenon in question. The flowers are protandrous; the anthers in the bud are contiguous to the short style and closed stigma, and, when they open, their pollen is deposited upon those organs. Upon the expansion of the corolla, the pollen is available for other flowers through the agency of insects. Somewhat later the stigmatic lobes part, and if after this insects visit the flower, they brush against the receptive spots of the stigma, and may dust them with extraneous pollen. Lastly, the two stigmatic lobes curl back until the receptive tissue upon their upper surfaces reaches the residue of pollen still sticking to the short style.

Much less common modes of operation are for the revolute stigmas to take the pollen from the edge of the tube of connate anthers, from hairs on the corolla, from bristles on the pappus, or from depressions in the petals. The case of abstraction

of pollen by stigmas from the edge of the anther-tube I observed in several Composites, as, for instance, in the species of the genera *Adenostyles* and *Cacalia*, and in *Arnica montana*. The external surface of the style in *Adenostyles* is beset with papillæ, which give it the rough glandular appearance whence it derives its name of Adenostyles (=glandular style); it has no collecting-hairs, and the pollen is therefore not swept but squeezed out of the anther-tube. The edge of the tube is furnished with prongs, each of which is slightly revolute and is concave almost to the extent of being boat-shaped, so that it is able to retain some of the extruded pollen. This pollen is only used for autogamy in the event of the stigmas not being dusted in any other way. In that case the two style-branches roll back until the receptive

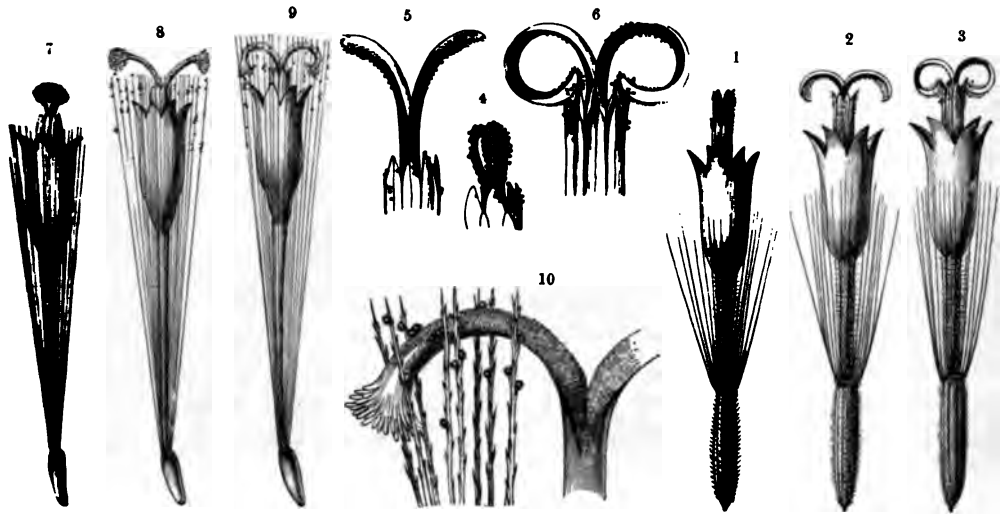

Fig. 303.—Autogamy effected by means of an inflection of the style-branches.

[1], [2], [3] Flowers of *Arnica montana* in successive stages leading to autogamy. [4] Style-branches of *Arnica* in contact shortly after their extrusion from the anther-tube. Pollen is clinging to the collecting-hairs and to the mouth of the tube. [5] The style-branches projecting still further from the tube and diverging from one another. [6] The style-branches curved back so as to bring the stigmatic tissue into contact with the pollen sticking to the tube of anthers. [7], [8], [9] Flowers of *Senecio viscosus* in the successive stages of development leading to autogamy. [10] A revolute style-branch of *Senecio viscosus* with its stigmatic tissue in contact with the pollen sticking to the bristles of the pappus. All the figures magnified.

tissue comes into contact with the edge of the anther-tube. The style-branches in *Arnica montana* (see figs. 303 [1, 2, 3, 4, 5, 6]) have collecting-hairs on the surface of their slightly-thickened tips only, and in this case the pollen is regularly swept out (figs. 303 [1] and 303 [4]). A small quantity of the pollen is always left behind upon the 5-toothed edge of the anther-tube. The manner in which the pollen is transferred to the stigmatic tissue by means of the re-volution of the style-arms is shown in the accompanying figure 303 [6].

As illustrations of the abstraction of pollen from the hairs of the corolla we may take a campanulate, a labiate, and two caryophyllaceous species. The corolla of the Nettle-leaved Bell-flower (*Campanula Trachelium*) has a thick coating of hairs on its inner surface. In the bud these hairs are directed horizontally towards the axis, and touch the style and the anthers. The deposition of the pollen upon the stylar column takes place in the same way as it does in the Bell-flowers already

discussed (see p. 361), but the moment the anthers are retracted some pollen is invariably caught by the hairs of the corolla, and when the flower opens a portion of the pollen is always to be seen adhering to them. The humble and hive bees which visit the flower may, of course, bring about cross-fertilization, just as they do in the other Bell-flowers. The style-branches in *Campanula Trachelium* do not, at the close of the flowering period, roll back so far as the central column; a less degree of bending is here adequate to bring the receptive tissue on the tips of the style into contact with the pollen sticking to the hairs.

In *Dianthus neglectus*, a species of Pink indigenous to the Southern Alps, and in the Glacier Pink (*Dianthus glacialis*), the laminæ of the petals are beset with hairs. The pollen is first exposed to the chance of dispersal by insects, but afterwards the stamens curve outwards, and some of the pollen becomes affixed to the hairs of the petals, which usually receive in addition a small deposit as a result of the scattering action of insect-visitors. The flowers are protandrous. The stigmas, which are situated in front of the entrance to the floral interior, wait till the period of the flower's bloom is nearly at an end, for the chance of being touched by insects bearing extraneous pollen. But sometimes no insects come, and in that case the pollen stored upon the hairy laminæ of the petals is made use of at the last moment. The transparent papillose stigmas wind themselves into the shape of the letter S, and, sweeping like a brush over the petals, collect the pollen from them. This operation is materially assisted in both the Pinks under discussion by the fact that the laminæ of the petals grow some millimetres longer during the flowering period, the result of which is to bring the hairs besmeared with pollen a little nearer to the stigmas. In *Dianthus neglectus* there is besides an involution and uprising of the laminæ in the evening, which, likewise, assist the process of sweeping up the pollen by the stigmas.

In *Ballota nigra*, a Labiate with protandrous flowers which grows commonly in hedges on cultivated land, some of the pollen falls at the very commencement of the flower's bloom upon the hairs clothing the borders of the upper lip. If no pollen is brought by insects to the stigma of a flower of this plant, the lower style-arm bends down at the end of the flowering period and takes up the pollen from the hairy mantle above referred to. The same kind of thing happens in a few other Labiates, as, for instance, in *Salvia viridis*, of the Mediterranean flora, whose style bends down in the event of a failure of insects, and brings the stigma into contact with a store of pollen resting upon the under-lip, where it fell at the very commencement of the flower's bloom. I have hitherto observed only in the cases of *Tozzia alpina* and *Pyrola media* the phenomenon of a style curving down to take pollen from cup-shaped hollows in the corolla in which it has lain stored, but it probably occurs in many other plants besides.

The curious case of the pollen being taken from the hairs of the so-called pappus by the stigma is illustrated in figs. 303 [7, 8, 9, 10]. In the Stinking Groundsel (*Senecio viscosus*), which will serve for an example, the style-branches are furnished at the tips only with bunches of collecting-hairs. As the style elongates these hairs sweep

the pollen out of the tube of anthers and leave it in a round lump at the top of the tube (see fig. 303[7]), whence it may be carried off by insects. At this stage the corolla and the hairs of the pappus are 6 mm. long. Soon afterwards the two style-branches, which have undergone rapid elongation, part asunder, and the pollen, if not already removed by insects, is shaken off, and falls on to the pappus-hairs, where it is caught by the asperities on their surfaces (see fig. 303[8]). The receptive tissue on the inner faces of the style-branches, which are now the upper surfaces, are in a position to get dusted with pollen brought by insects from other flowers. Meanwhile an elongation of every part of the flower has taken place; the pappus-hairs have attained a length of 7 mm., and the corolla of 6·5 mm. Lastly, the flower enters upon its third stage of development. The two style-branches curve down, bringing the stigmatic tissue into contact with the pollen sticking to the pappus-hairs, which have by that time grown another millimetre, and are therefore reached all the more easily, as they even project above the arms of the style (see figs. 303[9] and 303[10]).

In all the cases hitherto dealt with the only parts of the flower which are concerned in bringing about autogamy are the stamens and pistils. The filaments in some instances, the parts bearing stigmatic tissue in others, undergo inclination or inflection, whilst sometimes both organs mutually approach one another. No direct part in the process of autogamy is taken in any of these plants by the whorls of petals surrounding the stamens. We will now proceed to describe cases in which the petals are instrumental in effecting self-fertilization.

The simplest case of the discharge of this function by *petals* is to be found in flowers which are in the shape of tubes, cups, or basins, and whose anthers are adnate to the inner surfaces of the petals, and are brought into contact with the stigma in consequence of a contraction or closing together of the corolla—*Thymelœa Passerina*, a low shrub belonging to the Thymelaceæ, will serve as an example. The small inconspicuous flowers of this species contain nectar, and by its perfume attract insects which brush pollen from the anthers as they suck the honey and convey it to the stigmas of other flowers. The anthers are adnate to the inner face of the cup-shaped perianth, and are at first at a distance of only ½ mm. from the stigmas. Notwithstanding this proximity the viscid pollen is not spontaneously transferred to the adjacent stigma when the flower is first open. It is not till the flower is nearly over that a slight contraction of the upper third of the perianth causes the anthers to be pressed against the stigma, which stands at the same level as themselves. In *Claytonia perfoliata*, one of the Portulaceæ, autogamy is effected in the same manner, the only difference being that the anthers are borne on special filiform filaments which are adnate to the bases of the petals. These filaments, however, share in all the petals' movements, and the anthers at their extremities are pressed exactly upon the stigma when the corolla closes up.

In other cases the epipetalous stamens hold their anthers at the commencement of the flowering period underneath or behind the stigmas, and are pushed upwards during the flowering period by an elongation of the petals, in consequence of which

they rest in the last stage against the lateral edges of the stigmas. This process is very common in plants of the order Solanaceæ (*Hyoscyamus, Lycium, Nicotiana, Physalis, Scopolia*), and it has also been observed in Gentianaceæ (e.g. *Erythræa pulchella, Gentiana campestris, G. glacialis*). In some of these plants the elongation undergone by the corolla-tube is very considerable as compared with the size of the flower. In the American Tobacco plant (*Nicotiana Tabacum*) it amounts to nearly ½ cm., whilst in the little Centaury (*Erythræa*) it is only 2 mm. The elongation of the corolla-tube is accompanied in most instances by a stretching of the filaments. In consequence of this combined growth the anthers are, in the case of the short-styled flowers of *Lycium barbarum*, raised ½ cm. in 24 hours. In the Henbane (*Hyoscyamus niger*) the anthers are 7 mm. lower than the stigma in the morning when the flower is nearly open, but by the evening of the same day the simultaneous elongation of the corolla-tube and of the stamens adnate to it has raised the anthers to the level of the stigma and pressed them upon it. It is scarcely necessary to mention that in these plants, which are all protogynous, cross-fertilization is possible in the first part of the flowering period, and it is as a matter of fact very frequently effected through the intervention of insects.

A very curious variety of the phenomenon in question is exhibited by the large-flowered species of the Eyebright genus (*Euphrasia Rostkoviana, E. versicolor, E. speciosa*), and by the allied Yellow Rattles (*Rhinanthus angustifolius* and *R. hirsutus*). The flowers of these plants face sideways, and the corolla has a tri-lobed under lip and a bi-lobed helmet-shaped upper lip. Four stamens of the pollen-sprinkling type, which we have compared to sugar-tongs, are adnate to the corolla-tube. The anthers are concealed beneath the upper lip; the long filiform style is in the shape of the letter **S** and lies above the anthers, and when the flower is first open it projects considerably beyond them (see fig. 277 [4], p. 273). Stigma and anthers are then so placed as to make it inevitable that insects which enter the flower shall first touch the stigma, and the next moment become dusted with a shower of pollen from the anthers. If several blossoms are visited in succession cross-fertilization is certain to take place. If, however, insects stop away, the tube of the corolla elongates and carries up with it the epipetalous stamens. As the style retains its original length, the terminal stigma, which hitherto has projected in front of the anthers, now rests by the side of the anthers or just above them. Thus the stigma is in a sense overtaken by the anthers. In the large-flowered species of Eyebright the tense style then presses upon the anthers, forces them asunder, and, sinking down, brings its stigma between the anther-valves, where it cannot fail to get coated with the pollen of which they are still full. In the species of Yellow Rattle above mentioned, the stamens become flaccid towards the end of the flower's period of bloom and the pollen falls out and is left sticking to the hairs of the anthers or to the involute folds of the corolla, so that the style in brushing by usually removes it.

It is much less common for the *calyx* to play this part in bringing about autogamy. *Tellima grandiflora*, a North American Saxifragacea, is the only case

known at present in which the stigma after being at first rather higher than the anthers is overtaken by them and besmeared with pollen owing to an elongation of the calyx and consequent raising of the stamens, which are adnate to the tube of the calyx.

In many plants autogamy depends upon the fact that as the corolla falls off, its tube slips over the stigma, so that the latter rubs against the anthers, which are still laden with pollen, or against the inside of the corolla, which is also besmeared with that substance. This process presupposes that when the flower is in full bloom the anthers are overtopped by the stigma, and that the latter is still in a receptive condition at the time the corolla becomes detached and drops. Both these conditions are as a fact fulfilled in all plants of this category. In the species of the genus *Gilea* (Polemoniaceæ), and in the Brazilian plant *Psychotria leucocephala* (Rubiaceæ), the long filiform styles branch into divergent arms, which bear the delicate stigmatic tissue; and at the period of full bloom, these style-arms project far above both the limb of the corolla and the anthers. Consequently, insects alighting on these flowers encounter first of all the stigmas, and if they are laden with foreign pollen they occasion cross-fertilization. There is, on the other hand, in this form and position of the stigmas the further advantage, that, in case of a dearth of insect-visitors, the stigma may still acquire a supply of pollen when the corolla falls off—that is, at the very last moment of flowering. It is not unusual in these plants to see the corolla, after it has become detached, hanging for quite a long time from the long style and divergent stigmas, and this delay in the process of severance must materially assist the accomplishment of autogamy. The detached corolla persists in a similar manner in flowers with capitate, or short-lobed stigmas, as, for instance, in *Rhododendron hirsutum*, in *Digitalis*, *Anchusa*, *Cestrum*, and various other Scrophulariaceæ, Boraginaceæ, and Solanaceæ. In the case of *Rhododendron hirsutum*, as the corolla slips along the style, the stigma brushes off the pollen, which has invariably been discharged from the anthers before the flower opens and been caught upon the hairs in the interior of the corolla-tube. In *Cestrum aurantiacum*, the anthers, which are borne upon stiff and slightly-inflexed filaments, are pressed against the style, and the corolla is left hanging from the style, usually for a couple of days after its detachment, and does not fall till after fertilization has taken place, when the style also drops off. A great variety of contrivances exists with the object of promoting this method of autogamy by means of a falling corolla. A brief account of three of them will now be given. The flower of the Moth Mullein (*Verbascum Blattaria*), which may be taken as the type of a large number of flowers of Scrophulariaceæ, has a corolla with a very short tube and the limb spread out at right angles to it (*rotate*). Adnate to the tube are five stamens clothed with woolly hairs of a violet colour. The three upper stamens are a little shorter than the two lower ones, and all of them project obliquely beyond the limb of the corolla. The central style is still further exserted, and serves as a perch for insects to alight upon. It is obvious that so long as the parts of the flower are disposed in this manner every insect which arrives with a supply of

pollen must effect cross-pollination. As in so many other cases, autogamy is reserved for the last moment of bloom. With a view to its ultimate achievement, the two longer filaments cross themselves over the mouth of the corolla-tube in somewhat the same attitude as a pair of folded arms. This brings their two anthers, which are still full of the orange-coloured pollen, behind the stigma. The corolla now becomes detached from the receptacle and falls forward, but remains for a short time suspended to the long style, where it undergoes slight torsion. Finally, it drops with a gyratory motion, and as it does so the stigma must inevitably be brushed by one or other of the anthers lying in front of the mouth of the flower. The Pimpernel (*Anagallis*), which belongs to the order Primulaceæ, has a corolla resembling that of the Moth Mullein in being rotate and in containing five stamens clothed with violet hairs. The stamens in this case are very long, and the style is bent to one side, and passes between two of the stamens. Thus the stigma is out of reach of the anthers, and cannot, in the first stage of the flower's development, be dusted with their pollen. On the other hand, cross-fertilization may be effected by the small insects which creep over the flat limb of the corolla in order to feed on the hairs of the stamens. The flowers of the Pimpernel belong to the category of those in which the corolla opens and shuts periodically. The operation of closing is due to the expanded limb being thrown into superincumbent folds. On the second occasion of the flower's closing, the anthers come into contact with the part of the corolla that is folded in, and leave some of their pollen sticking to it. This pollen is still to be seen adhering to the inner face of the corolla on the following day, when the limb expands again, and there it remains till the evening, when the corolla closes for the third time. After this the corolla does not open any more, but falls off still closed, and, as it does so, brushes the style, which is held between two stamens, and leaves upon the stigma the pollen that was sticking to its inner surface. Again, there is the case of *Soldanella alpina*, to which we have already several times had occasion to refer in other connections, and also as affording an instance of a second form of autogamy (p. 333) besides that now in question. The style stands up in the form of a column in the middle of the bell-shaped corolla, and has the five stamens close to it. The anthers are united into a cone, and act as sprinklers in the dispersion of their pollen. When an insect pushes into a flower it rubs first against the stigma, and dusts it with foreign pollen, and as it forces its way further in it displaces the various parts composing the cone of anthers, and is consequently besprinkled with pollen. If no insects visit the flower the anthers are still full of pollen when the time comes for the corolla to drop off, and as the style is drawn through the dislocated cone of anthers, the pollen in the interior of the latter is caught up by the stigma, and self-fertilization is effected.

Next to these plants, in which autogamy takes place on the fall of the corolla owing to its tube slipping over the stigma, there comes a group of species in which the same result is attained in the following manner. At the time when the flower opens, the petals are slightly smeared with pollen, and this deposit forms a reserve store. Should the stigma not have received any pollen from extraneous sources, the

flower being nearly over, certain movements are undergone by the petals which result in the transference of the pollen sticking to their surfaces, margins, lobes, or folds, as the case may be, to it. The instances of this mode of effecting autogamy are very numerous, and it will be best to class them in small sub-groups, and to take a well-known example from each as an illustration.

In *Argemone*, *Hypecoum*, and *Specularia*, which will serve as types of the first group, there is no considerable elongation of the pollen-flecked petals during the

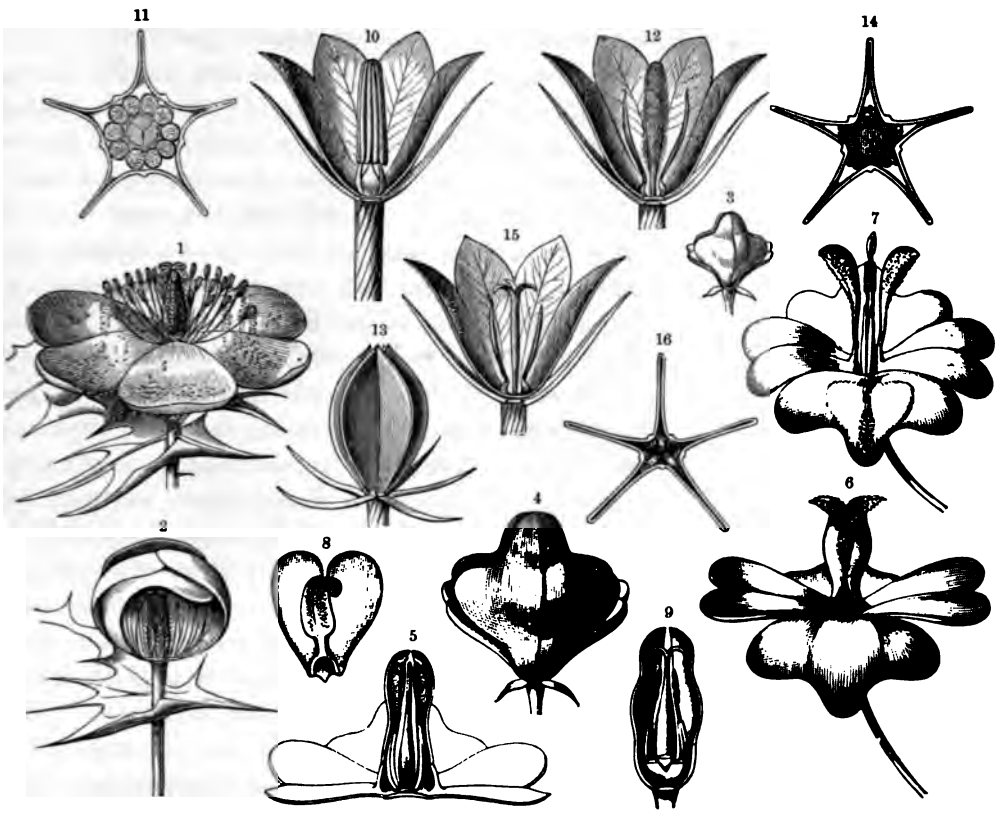

Fig. 304.—Autogamy effected by the petals.

[1] Flower of *Argemone Mexicana* open in the sunshine. Pollen which has fallen from the anthers is resting upon the concave petals. [2] The same flower closed; one of the petals besmeared with pollen is laid upon the stigma; the front petal is removed. [3] Closed flower of *Hypecoum grandiflorum*, natural size. [4] The same magnified. [5] Longitudinal section through the open flower in the first stage of development. [6] Open flower in which the pollen-laden lobes of the inner petals are beginning to separate. [7] The same flower at a later stage. [8] One of the two inner petals; the middle lobe is coated with pollen; at its base is the pit containing the honey. [9] Longitudinal section through a closed flower in its last stage of development. [10] *Specularia speculum*; longitudinal section through an open flower in the first stage. [11] Transverse section through a closed flower in the first stage. [12] Longitudinal section through an open flower in the second stage. [13] Closed flower. [14] Transverse section through a closed flower in the second stage. [15] Longitudinal section through an open flower in the last stage. [16] Transverse section through a closed flower in the last stage. [1], [2], [3] natural size; the rest magnified.

period of the flower's bloom. This period is only a single day in the case of *Argemone*, and the process takes place in a very simple manner. In the morning, as soon as the petals are wide open and the tension of the sheaf of stamens surrounding the pistil is somewhat relaxed, there is an immediate fall of pollen on to the concave surfaces of the petals (see fig. 304[1]). The flowers are erect, as also is

the pistil, and the stellate stigma, which offers the best alighting place for insects, rests at a slightly higher level than the anthers, and at a sufficient horizontal distance from them to prevent their pollen from reaching, spontaneously, its receptive tissue. In the course of the day insects arrive with pollen from other blossoms and cause cross-pollination. When the evening comes the petals close up over the pistil, and one of them brings its inner surface, which is covered with pollen, into direct contact with the stigma (see fig. 304[2]).

The case of the *Hypecoum* is far more complicated. The flowers of this plant have two small sepals and four large tri-lobed petals (see figs. 304[3] and 304[4]). The latter are arranged in two pairs at right angles to one another, one pair being inserted a little higher than the other. The middle lobe of each of the petals belonging to the upper pair is curiously modified; its surface is concave, and in the young flower has the shape of a spoon with fringed edges. The function of these lobes is to collect all the pollen from the anthers at the very commencement of flowering. The anthers are, like those of Compositæ, coherent into a tube inclosing the style; but instead of opening inwards as the latter do, they are extrorse, *i.e.* dehisce outwards. At the time of dehiscence and of the discharge of the pollen the two spoon- or pouch-shaped central lobes of the upper petals are in close proximity to the anthers, and they receive the whole of the pollen (see fig. 304[5]). After this transfer has been accomplished the two lobes now containing the pollen separate from one another, the first parts to disunite being the free extremities at the top, then the lateral edges (see fig. 304[6]). The pollen is thus exposed and may be carried off by insects which come for the honey concealed in a little depression at the base of each lobe (fig. 304[8]). The two linear stigmas being in close contact at this stage, their tissue is not as yet accessible; they do not disunite till two days after the first opening of the flower, but when that interval has elapsed they diverge, and then constitute the most convenient place for insects to settle upon. They are now in exactly the same position as was previously occupied by the pollen-laden lobes (see fig. 304[7]), and therefore if an insect alights upon them after visiting younger flowers, it is sure to dust the stigmatic tissue with foreign pollen. Meantime the petal-lobes which received the pollen become much more reflexed, especially at their lateral edges; the back of each lobe, which was originally convex, is now deeply concave like a boat, and the whole structure is in a manner turned inside out. The direction of the two divergent stigmas is at right angles to the two upper petals, and their tips point towards the median line of the two outer ones. In consequence of this arrangement the stigmas are at such a distance from the pollen on the lobes that no autogamy could take place without some special intervention. The requisite assistance is afforded by the two outer or inferior petals, and their mode of action is as follows. When evening comes the flower closes; the two lateral pollen-free lobes of each superior petal rise up first of all, and then the two inferior tri-lobed petals wrap themselves over them (see figs. 304[3] and 304[4]). On the second or third day, when the margins of the pollen-laden lobes have curled back, contact ensues between the two closed petals and the revolute

margins of these lobes, and some of the pollen sticks to the petals, so that next day when the flower opens again a streak of pollen may be seen along the middle line of each of the outer petals (see fig. 304[7]). On the last day of bloom the two stigmatic arms curve down, and when the flower closes once more at dusk, they, being directed towards the median lines of the outer petals, are brought into contact with the pollen adherent along those lines (see fig. 304[9]), and thus at the last moment autogamy is effected.

The flowers of the Venus's Looking-glass (*Specularia speculum*, see figs. 304[10, 11, 12, 13, 14, 15]) are protandrous like those of the common Bell-flower (*Campanula*); their anthers form a tube in the newly-opened flower (see figs. 304[10] and 304[11]), dehisce inwards and deposit the whole of their pollen on to the delicate hairs which clothe the external surface of the stylar column. When the tube of anthers breaks up through the shrivelling of their empty lobes, an axial column covered with pollen is exposed to view, and is used by insects as an alighting place. For the present pollen can only be taken away—not deposited—by insects, for the style-arms are still united, and the receptive tissue is inaccessible. Every evening the erect basin-shaped corolla folds up longitudinally in such a manner as to form five re-entrant angles (see fig. 304[13]). The in-folded angles of the corolla reach inwards as far as the central column (see fig. 304[14]), and get besmeared with some of the pollen with which it is coated. The next morning when the corolla opens linear streaks of pollen may be seen upon its internal surface. Meanwhile the three short arms of the style have disunited and spread themselves out, whilst the pollen has fallen off the stylar column (see fig. 304[15]), or been carried away by insects. If at this stage insects alight on the divergent style-arms fresh from visiting younger flowers, cross-poilination is certain to ensue. As night approaches the flower closes in the same way as on the previous evenings, and the pollen sticking to the lines of the internal folds comes against the style-arms, which are spread out and slightly reflexed (see fig. 304[16]), and thus effects self-pollination. In the event of the stigmatic tissue having already received a deposit of foreign pollen, this act of self-pollination is superfluous, but otherwise the process is effectual, and always results in the formation of fruit. A similar phenomenon may be observed in the nodding or pendent flowers of various Solanaceæ, particularly in the Potato plant (*Solanum tuberosum*), for here also there is frequently a transference of pollen to the corolla, and from the folds of the corolla to the stigma. But in this case the pollen issues from the anthers through terminal pores, and falls irregularly and not necessarily upon particular parts of the corolla, so that autogamy is not so certain to take place in these plants as in *Specularia*.

From the above descriptions it will be seen that in *Argemone*, *Hypecoum*, and *Specularia*, although the corolla is the part of the flower which is instrumental in effecting autogamy, the process does not involve any noticeable elongation of the pollen-besmeared corolla during the period of flowering. We have now to deal with another group of plants in which the petals perform just the same function as in the foregoing cases with respect to autogamy, but in which a very important part

of the operation consists in an elongation of the corolla. Types of this group are afforded by Gentianaceæ of the subdivision Cœlanthe (*Gentiana asclepiadea, G. Pneumonanthe,* &c.), Liliaceæ (*Colchicum*), Amaryllidaceæ (*Sternbergia*), Iridaceæ of the genus *Sisyrinchium,* and those Composites whose capitula are furnished with ligulate florets (*Crepis, Hieracium, Hypochœris, Leontodon,* &c.).

Gentiana asclepiadea (see fig. 305) is one of the sub-alpine species of the Baltic flora, and has protandrous flowers. The anthers are united into a tube, as in the case of Composites and Bell-flowers. They do not, however, discharge their pollen into the tube, but behave in this respect in the same manner as those of *Hypecoum,* that is to say, they open by longitudinal fissures down their external faces, so that after dehiscence the outside of the anther-tube is covered all over with pollen

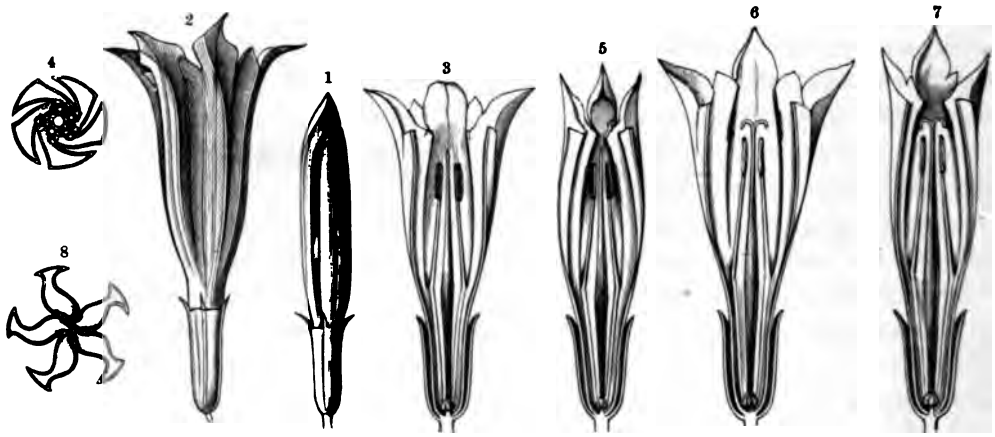

Fig. 305.—Autogamy effected by means of the corolla.

[1] *Gentiana asclepiadea.* Flower-bud shortly before it opens for the first time. [2] Open flower in the last stage of development. [3] Longitudinal section through a flower which has just opened for the first time. [4] Transverse section through the same flower. [5] Longitudinal section through a flower closed for the first time. Pollen is affixed to the edges of the folds into which the corolla is thrown. [6] Longitudinal section through a flower which has opened for the last time. [7] Longitudinal section through a flower which has closed for the last time. The pollen is being transferred from the folds of the corolla to the reflexed stigmas. [8] Tranverse section through the same flower. The anther-tube in [3], [5], [6], and [7] is represented in optical section.

(see fig. 305 [3]). The linear style-branches bearing the stigmatic tissue are at this stage closely united and as yet immature. Humble-bees are attracted in large numbers by the rich store of honey in the floral interior, and as the funnel-shaped corolla is wide open in the daytime the insects enter, and are often entirely engulfed in the flower. If the visit is paid to a young, newly-opened flower the insect loads itself with pollen by coming into contact with the tube of anthers. Two days later the linear stigmas separate and curve over downwards. Their position now renders it inevitable that they should be touched by the bees, of which a large number continue to visit the flower, there being still plenty of honey in it. If these visitors have recently visited younger flowers they are sure to effect cross-fertilization. The corolla is disposed in peculiar folds, as is shown in figs. 305 [1] and 305 [2]; to describe them sufficiently briefly for our present purpose would not be possible. When the flower expands in the morning these plaits open out; at sunset they are again drawn in towards the middle of the funnel, and at the same time a movement

of torsion takes place which brings the folds into the position shown in transverse section in fig. 305[4]. The re-entrant angles come into direct contact with the surface of the anther-tube (see figs. 305[4] and 305[5]) and take from it some of the pollen, which is very adhesive. On the next day, and on the third and fourth days, the flower opens and shuts again. During that time almost every part of the flower grows in length; the filaments gain 1 mm., the pistil 3 mm., and the inferior half of the corolla as much as 5 mm. In consequence of this growth the pollen transferred to the folds of the corolla from the anther-tube is raised 5 mm., and rests at the same level as the stigmas, which have in the meantime become divergent. When darkness sets in, and the corolla once more falls into folds and closes up, the pollen affixed to the re-entrant angles is transferred to the stigmatic tissue. The process is greatly facilitated by the fact that, at this final stage of flowering, the internal folds assume a somewhat different form and position (see fig. 305[8]), for in consequence of this change the parts besmeared with pollen are brought still nearer to the middle of the flower. This marvellous contrivance for promoting autogamy may also be observed in *Gentiana Pneumonanthe*, a species which grows in damp meadows in England and all over the continent of Europe, and in this instance the elongation of this funnel-shaped portion of the corolla in the interval between the first and last occasions of the flower's closing amounts to some 7 mm.

The phenomenon occurs in a much simpler form in *Sternbergia* and *Colchicum*, belonging to the orders Amaryllidaceæ and Liliaceæ respectively. The flower of *Sternbergia lutea* has an erect funnel-shaped perianth composed of six segments, three of which are rather longer than the other three. The six upright stamens have nectar secreted at their bases, and are adnate to the segments of the perianth; they are arranged in two whorls round the styles, and have their anthers turned outwards. The styles rise up in the middle of the flower in the form of three long threads. The stigmas, in which the styles terminate, are higher than the anthers throughout the period of bloom, and as, after the dehiscence of the anthers, the pollen adheres to the internal walls of the loculi, it is not spontaneously transferred to the stigmas in the same flower. The flowers are protogynous, and at the commencement of their bloom are adapted to cross-pollination through the agency of insects. Even after the extrorse anthers have dehisced, insects entering the blossom in quest of honey brush first against the stigmas, and only subsequently come into contact with the anthers resting at a lower level. The perianth is open in the daytime alone; in the evening its segments close together so tightly that their inner surfaces touch the extrorse anthers and become smeared with pollen. This happens the very first evening following on the dehiscence of the anthers. The pollen affixed to the perianth-segments does not reach the level of the stigmas till the following day. Its ascent is due to an elongation of the lower regions of the perianth-segments. There is a simultaneous growth of the other parts of the flower, but it is surpassed by the extraordinary increase in the length of the perianth-leaves. Whilst the styles grow 4 mm., and the stamen-filaments from 9 to 10 mm., these segments grow 18·5 mm. Afterwards, when the

perianth closes for the night, the pollen is transferred from the inner faces of its segments to the stigmas. Two subsidiary circumstances co-operate in bringing about this act of autogamy. The first is, the fact that the free extremities of the styles which bear the stigmatic tissue curve outwards when the flower's end approaches, and the second is, the circumstance that the excessive elongation is especially marked in the three perianth-segments which are opposite the stigmas.

The same events take place in the flowers of the Meadow Saffron (*Colchicum autumnale*). Anyone crossing a meadow in the autumn in which this plant is growing may see what a great difference exists between young and old flowers in respect of the length of the perianth-segments, and can easily convince himself of the connection between this diversity and the operation of autogamy as explained above. In the Meadow Saffron the phenomenon is somewhat complicated by the circumstance that heterostylism (see p. 302) plays a much more important part in this instance than in the other Liliaceæ. *Colchicum* possesses long-styled, mid-styled, and short-styled flowers, which all grow promiscuously together in one and the same meadow, and the elongation of the perianth-segments is anything but uniform in these three forms. Careful measurements of some five hundred specimens gave the following remarkable result. In long-styled flowers the three longer perianth-segments grow 9 mm. and the three shorter 12·6 mm.; in short-styled flowers the longer segments grow 10 mm. and the shorter 15 mm., and in the mid-styled flowers the longer segments grow 13·5 mm. and the shorter 18·5 mm. I shall return to the subject of heterostylism again presently, and shall then have an opportunity of entering more fully into its significance; at present it is only necessary to mention that the stigmas of the short-styled flowers, when the latter are nearly over, come into contact not only with the pollen sticking to the perianth-segments, but also with the tips of the anthers themselves, for in this form there is a proportionate growth of the filaments.

This same process, which in *Colchicum autumnale*, in Sternbergias and in Gentians of the Cœlanthe tribe only culminates in autogamy after the lapse of a week, is accomplished in the delicate plant *Sisyrinchium* of the order Iridaceæ in the course of a few hours. Apart from their ovaries, which are inferior, the flowers of *Sisyrinchium* are constructed similarly to those of Liliaceæ. The three small petaloid stigmas, in which the styles terminate, project above the anthers. The latter are coherent into a tube and open extrorsely, whilst the flower is still in the bud state, and the consequence is that some of their pollen is affixed to the contiguous leaves of the perianth. The flower opens out into a cup, and insects may then cause heterogamy; but on the approach of evening the perianth closes again, and autogamy takes place owing to the fact, that in the course of those few hours the petals have lengthened exactly enough to bring the pollen sticking to their inner surfaces to the level of the stigmas.

Reference must also be made to those Composites in which autogamy is brought about by means of an elongation of the ligulate corolla, and the consequent uplifting of the pollen adherent to it. In most and probably in all species of *Crepis*, *Hiera-*

cium, *Leontodon*, and *Hypochœris*, in whose capitula the peripheral ligulate florets are considerably longer than those of the centre, it is easy to see that when the capitula close in the evening the ligulate petal in each flower rises up and lays its inner surface upon the pollen which has been extruded from the tube of anthers in the course of the day. The pollen remains sticking to the petal during the two succeeding days, and in the meanwhile the latter grows about a couple of millimetres in length and carries the pollen up with it. At the same time the style undergoes elongation and protrudes out of the top of the tube of anthers, holding its two arms, which are now divergent and expose the receptive stigmatic tissue

Fig. 306.—Autogamy effected by means of the corolla.

[1] *Pedicularis incarnata*. [2] A flower of *Pedicularis incarnata* which has just become accessible to insects. [3] Longitudinal section through the same flower. [4] The same flower in a later stage of development. [5] Longitudinal section through the flower of [4]. [6] The same flower shortly before the corolla fades; the upper lip is bent down and the mealy pollen falling out of the loosened valves of the anthers is trickling through the tubular upper lip upon the stigma stationed in front of the mouth of the tube. [7] Longitudinal section through the flower of [6]. [1] nat. size; the other figures double their nat. size.

upon their surfaces, at the same level as the pollen sticking to the ligulate corolla. When next the capitulum closes, the pollen is transferred to the stigmas, and autogamy ensues. This adaptation of the marginal florets of the capitula is all the more interesting, seeing that in the central florets in the same plants, geitonogamy has been found invariably to prevail (*cf.* p. 319).

One of the most curious contrivances for effecting autogamy consists in a special inflection of the corolla, on the termination of the flower's period of bloom, enabling it to conduct the pollen which falls from the anthers to the stigmas. The pollen in these cases is of mealy consistence. Two species of the Lousewort genus (*Pedicularis*) may be used to illustrate this form of adaptation, and we will first take

Pedicularis incarnata (see fig. 306), a species which grows abundantly in Alpine meadows. The flowers of this plant are arranged in spikes, and their development proceeds from below upwards (fig. 306 [1]). The corolla is bilabiate; the lobes of the under lip are at first upturned (see fig. 306 [2]), but subsequently are expanded in a slanting plane (figs. 306 [4] and 306 [6]). The upper lip is helmet-shaped and rolled into a tube at the apex (figs. 306 [2, 3, 4, 5, 6, 7]). The stamens are of the sugar-tongs type, and their anthers are concealed underneath the arch of the upper lip (figs. 306 [3, 5, 7]). The long style is bent at an angle to correspond to the form of the upper lip; its anterior extremity passes through the tube and rests in front of the orifice and at the same time in front of the entrance to the floral interior. The humble-bees which make use of this entrance are obliged to rub against the stigma, and if they come laden with pollen from other flowers cross-fertilization ensues. Owing to the fact that the flowers are protogynous insect-visitors cannot, in the first stage of bloom (figs. 306 [2] and 306 [3]), carry off any pollen, but can only leave behind upon the stigma what they have brought with them; at later epochs, however, the insects, though still brushing first against the stigma, are next moment besprinkled with the mealy pollen which falls from the anthers in consequence of the disturbance of the tongs-like stamens. Under the galeate arch of the upper lip there is a slit (fig. 306 [4]) to allow the pollen to fall freely, and whenever an insect enters between the under and upper lips this gap is enlarged. The head is the part of the humble-bee that receives the pollen, and the latter may, of course, then be conveyed to other flowers. If no insects visit a flower, the pollen remains for rather a long time dormant in the anthers; but, in the last stage of bloom, the filaments become flaccid and give way, and the pollen then falls of itself upon the edges of the slit. At the same time the upper lip undergoes a marked downward bending (fig. 306 [6]), whereby that part of it which is prolonged into a tube, is brought into a vertical position, so that the pollen rolls down it, and is directed on to the stigma, which hangs right in front of the mouth of the tube (fig. 306 [7]). Sometimes the stigma is drawn into the tube in the process of bending above referred to and sticks there, like a cork in the neck of a bottle; in which case self-pollination takes place inside the tube. Autogamy of the type exhibited in *Pedicularis incarnata* occurs with slight variations in all species which have the upper lip of the corolla produced into a tubular beak. The cases of this kind especially subjected to investigation were *Pedicularis asplenifolia*, *P. Portenschlagii*, *P. rostrata*, and *P. tuberosa*.

Very different behaviour is observed in several species of the same genus in which the upper lip has the form of a cowl or a helmet truncated in front, as, for example, *Pedicularis Œderi*, *P. foliosa*, *P. comosa*, and *P. recutita*. Of these we will take for illustration *Pedicularis Œderi*, which grows abundantly in Alpine meadows in the neighbourhood of the Brenner Pass in Tyrol. As regards the construction of its flowers, this species differs from *P. incarnata* in that the stigma is stationed in front of the truncated helmet forming the upper lip, and also in having projecting ribs on both sides of the corolla, which act like a system of levers in causing the inflection just before the flower fades. The entire upper lip at this

stage bends down so sharply as to look as if the flower had been wilfully broken. The back of the upper lip, which originally constituted a direct prolongation of the corolla-tube, now forms with it an angle of 60°, and later an angle of 90°. The movement is shared, of course, by the style and by the tongs-like stamens concealed beneath the upper lip. The consequence is that the stigma at the end of the style is no longer in front of the anthers, but underneath them, and that the anthers, which hitherto have been held tightly together, move asunder and let their pollen fall. The stigma is situated in the line of descent of the pollen, and, being very viscid, it catches a quantity of the particles of the shower, and thus secures the accomplishment of autogamy (*cf.* fig. 276, p. 272). The same changes of position, which, spontaneously initiated at the close of the flowering period lead to autogamy, may, curiously enough, be brought about at an earlier stage by the humble-bees which fasten on to the flower, but in that case they result in cross- and not self-fertilization. For a description of the processes involved the reader is referred to the account of them given on p. 272, where *Pedicularis recutita* is the species dealt with. We may here remark that the whole of the pollen which falls from the anthers in the last stage of flowering is not devoted to autogamy; the few pollen-cells which stick to the viscid stigma are sufficient for that purpose. A larger number of pollen-cells fall past the stigma into the air, where they may be caught up by a gust of wind, and carried away in the form of a tiny cloud of dust. If mature stigmas of other *Pedicularis*-flowers happen to lie in the direction in which the dust-cloud travels, individual cells of the cloud are left behind on these stigmas, and cross-fertilization thus ensues in the same way as in the flowers of the Toothwort (see p. 330).

Of the Rhinanthaceæ most nearly allied to the genus *Pedicularis* a few species of the Cow-wheat, which may be represented by *Melampyrum sylvaticum*, remain to be mentioned as instances of plants exhibiting the form of adaptation above described. The sole difference is that in *Melampyrum sylvaticum* the tube of the corolla bends at a sharp angle at a point only 2 mm. above the base, whilst the limb itself, composed of the lips, undergoes no independent flection. The result is the same as in those species of *Pedicularis* of which an account has been given, inasmuch as the pollen falls, in consequence of the inflection, from the anthers of stamens of the sugar-tongs type on to the stigma beneath.

A kindred process to the preceding consists in the anthers with their coating of pollen being brought into contact with the stigma by means of an inflection of the corolla. The pollen is not mealy in this case, but adhesive. No one who will take the trouble to examine the inflorescence in one of the twining species of Honeysuckle (*Lonicera Caprifolium*, *L. Etrusca*, or *L. Periclymenum*) can fail to notice that the corolla-tube, in buds which are about to open, ascends in an oblique direction, that in newly-opened flowers it is horizontal, and that, a short time before a flower fades, it is bent downwards. The angle through which the axis of the flower is displaced relatively to the flowering stem varies from 45° to 90°; in the case of horizontal stems it is less, and in that of erect stems greater, but the object invariably aimed at is that the open corolla shall, as night comes on, be disposed in

the most convenient manner possible for nocturnal moths to visit it. In flowers adjusted in anticipation of such visits, the stigma takes up a position which precludes the possibility of its being dusted with pollen from the anthers in the same flower. In the act of introducing their long probosces into the honey secreted in the interior of the flower, Sphingidæ come into contact first with the stigma and then with the anthers, and as they travel from flower to flower they are the means of effecting cross-pollination in this as in so many other cases. But should no moths come upon the scene, autogamy invariably takes place through the inflection of the corolla-tube already referred to. The stamens are adnate to the corolla-tube, and undergo inflection with it, thus bringing the anthers, still covered with pollen, into direct contact with the stigma, which, in the horizontal position of the flower, was stationed a little lower than, and in front of, the anthers.

In respect of the manner of their autogamy the last-mentioned plants exhibit a transition to a large group in which self-fertilization is prevented during the early stages of flowering by the relative positions of anthers and stigmas, but is effected towards the end of the period of bloom, when certain changes in the position and direction of the *flower-stalks* have taken place and brought the pollen and stigmas into conjunction. These alterations of position are usually associated with one of the many other contrivances already described. Thus, for instance, the styles or the filaments may undergo elongation and inflection, or the corolla may grow up and carry with it pollen affixed to its petals, or the stamens themselves, and so forth; but these processes would not of themselves be sufficient to induce autogamy if it were not for the part played by the flower-stalks. To put it briefly, the stigmas and the anthers become, in the absence of cross-fertilization, so situated by the growth and inflection of the flower-stalk as to render autogamy inevitable. When we consider that the changes in the position and direction of pedicels, and the consequent drooping or straightening up of flowers, serve other purposes of great importance in the life of plants, and that, in particular, to these inconspicuous movements are often due the protection of pollen from moisture and the placing of the entrance to a flower in the position most convenient to insects whose visits are profitable to the plant, we cannot be surprised to find that this form of adaptation is one of the commonest of all. A combination of advantages, either simultaneous or in rapid succession, is secured, and contrivances of this kind which best contribute to the economy of plant-life are found by experience to be invariably the most widely distributed.

We will first consider flowers in which the stigma begins by being situated outside the line of descent of the pollen as it falls from the anthers—a circumstance which is advantageous inasmuch as it favours cross-fertilization—but where subsequently the entire flower assumes a different position in consequence of a growth or an inflection of the flower-stalk, whilst the direction and situation of stamens, style, and stigmas remain the same as before. In several species of *Narcissus*, *e.g.* the graceful *Narcissus juncifolius*, and in some Boragineæ, such as the common Wood Forget-me-not (*Myosotis sylvatica*), the flowers at first have their mouths set

in a lateral direction; the stigma is stationed behind the anthers, and the pollen that falls out of the anthers does not come upon the stigmas so long as the corolla-tube is horizontal. During that period the branch of the inflorescence to which the horizontality of the corolla is due is curved, but it subsequently straightens out and raises the corolla-tube to a vertical position whereby the stigma is brought into the line of descent of the pollen as it falls from the shrivelling anthers. This occurs in *Tulipa sylvestris*, *Polemonium cæruleum*, *Saxifraga hieracifolia*, *Chrysosplenium alternifolium*, *Rhododendron Chamæcistus*, *Vaccinium*, *Arctostaphylos*, *Cerinthe*, *Symphytum*, and *Cyclamen*. The process may be most clearly traced in the various species of *Cyclamen*, which are at present so commonly grown in pots. The first day that the flower is open and the petals reflexed, the peduncle, which rises up from the ground, has its extremity bent over almost at a right angle. The short bent piece of the stalk is inclined at an angle of from 50° to 60° to the horizon. The variation in the size of the angle is due to the fact that the longer inferior part usually ascends obliquely from the ground, and is only in rare cases quite vertical. From day to day the angle of inclination may be seen to diminish by about 10° until at the end of the flower's period of bloom the short down-bent portion at the top and the long upright portion of the peduncle are almost parallel, and the whole has the form of a crook. As the style lies in the direct line of prolongation of the short piece of the peduncle and projects beyond both the tube of the corolla and the cone of anthers, autogamy cannot take place in the first stage of the flower's development, when the style is inclined at an angle of from 50° to 60° to the horizon. Insects visiting the flower at this period first brush against the stigma at the end of the projecting style, and may occasion cross-fertilization; but even if it should happen that the displacement of the anthers caused by an insect's intrusion has the effect of letting some of the pollen fall out, the shower does not descend upon the stigma, for it is not yet situated vertically beneath the anthers. Towards the close of the flowering period, on the other hand, the stigma is moved by means of the inflection of the peduncle above referred to into the path along which the pollen descends; the filaments become flaccid, the anthers disunite, and the pollen stored in the cone is sprinkled upon the still receptive surface of the stigma.

This will be the best place to describe the curious case of autogamy which is exhibited by the *Calceolaria Pavonii* of South America. The flowers of this plant are protogynous, and when first open they are borne on almost horizontal stalks. The anthers, which are still closed, are concealed beneath the shortly truncate upper-lip. The style bearing the already mature stigma is borne horizontally, its tip only being bent down like a hook at a short distance from the stigma (as is shown in figs. 307 [1] and 307 [2]) so as just to touch the roof of the inflated under-lip. The short-tongued Hymenoptera which come in quest of the honey secreted within the lower-lip make use of its roof as an alighting-place. The instant one of them settles upon it the lip drops as in the case of the Snapdragon, the movement being regulated by the powerful ribs on each side of the corolla. The result is

twofold: the jaws of the flower are set wide open and the honey-secreting lobe hitherto concealed in the hollow of the lip is brought out so as to enable the insect which has caused the movement to lick up the honey without difficulty. In doing so, however, it rubs its back against the stigma, and should it have previously visited older flowers cross-pollination ensues. These are the conditions at the commencement of flowering. The next day or the day after that, the anthers open by comparatively large pores, one at the top of each loculus. The connectives are articulated to the filaments, so that when the latter are pushed the anthers are set swinging and let fall some of their mealy pollen. If under these circumstances a rather large Hymenopter alights on a flower in quest of honey, he must necessarily knock against the filaments and be sprinkled by the pollen which descends in consequence, especially seeing that the filaments have meanwhile increased in length sufficiently to bring the upper lobes of the anthers upon the highest part of the arched external surface of the under-lip. If the flower is not visited by insects, a quantity of the mealy pollen falls of itself upon this convex surface (see fig. 307 [2]). Soon afterwards the flower-stalk curves down, causing a steep inclination of the roof of the under-lip, which still bears on its highest part the heap of pollen deposited by the anthers. The pollen slips down the inclined plane, and is thus brought into contact with the stigma, which still retains its receptive power (see fig. 307 [3]).

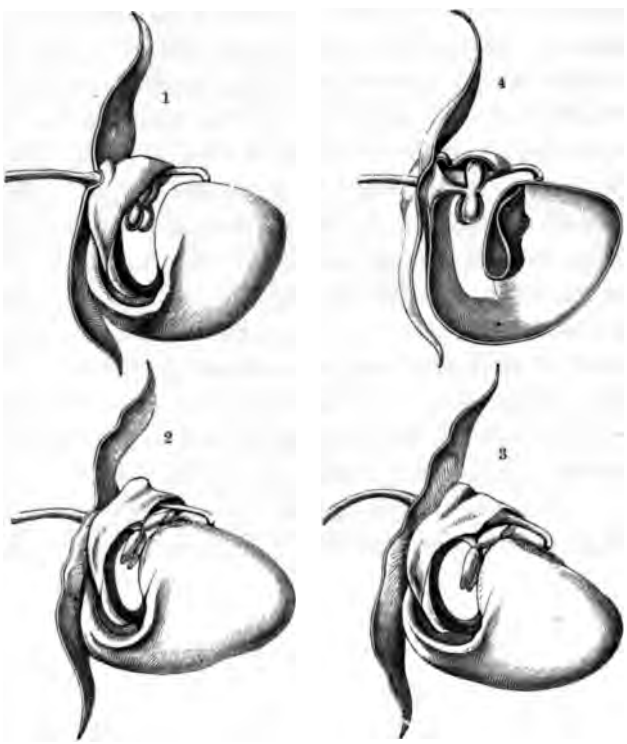

Fig. 307.—Autogamy caused by inflection of the flower-stalk and the adjustment of the under lip to form an inclined plane down which the pollen deposited upon the under-lip slides to the stigma: *Calceolaria Pavonii*.

1, 2, 3 Side view of the flower in the three successive stages leading to autogamy. 4 Longitudinal section through a flower in the first stage of development. All the figs. slightly magnified.

The acccomplishment of autogamy, by means of a *combination of movements and inflections* of the flower-stalks with similar action on the part of the stamens and style is of as common occurrence as it is varied in respect of details. The drooping Star of Bethlehem (*Ornithogalum nutans*) derives its name *nutans* from the attitude of its flowers, but the latter really do not assume that position until quite at the last; in the bud-stage they are erect, and even after the leaves

of the perianth have expanded the pedicels stand out horizontally from the axis of the inflorescence, and the flowers face sideways. The flowers are protandrous. The anthers of the three stamens, situated in front of the little pits in the ovary in which honey is secreted, dehisce at the same moment as the perianth-leaves expand, and these anthers are placed in such a position as to be touched by insects as they enter the flower. The stigma is still immature at this stage. A little later, when the stigmatic tissue has developed the power of retaining pollen, the stamens move out of the way of insects towards the periphery of the flower and thus render it possible for cross-pollination to be effected by such of these visitors as bring with them pollen from younger flowers. In the third stage of the flower's duration the pedicel bends down until the flower is at last truly nodding. The stamens have meantime executed a reverse movement towards the middle of the flower, and the stigma is found to be just underneath one of the anthers belonging to a stamen of the shorter class. These anthers always have some pollen left in them, for they do not open till the second stage of the flower's development and cannot have undergone contact with insects. The gradual shrinkage of the anthers now causes this store of pollen to fall out of them on to the adjacent stigma, and thus autogamy is effected just before the flower fades.

The hermaphrodite flowers of certain Rosaceæ — *Dryas octopetala*, *Geum coccineum*, *G. montanum*, *G. reptans*, *Potentilla atrosanguinea*, *P. repens*, and *Waldsteinia geoides*—and those of some Ranunculaceæ, viz., *Adonis vernalis*, *Anemone alpina*, and *A. baldensis* afford particularly instructive examples of autogamy. In all these plants the flowers are protogynous and are characterized by having a large number of carpels crowded together in the centre and surrounded by equally numerous stamens, which are disposed in several whorls. In the Rosaceæ in question the stamens are tucked down before the bud unfolds, and they do not straighten out until the anthers are nearly ready to open. Dehiscence occurs first in the anthers which belong to the outermost whorl of stamens, and are furthest away from the stigmas of the bunch of ovaries in the middle. This relative position of the two sets of organs excludes all possibility of autogamy, especially when the flower is erect; on the other hand, cross-pollination is quite likely to be effected by insects, which alight on the stigmas, thence proceed towards the circumference of the flower, licking up honey and collecting pollen on the way, and finally take wing from the edge to visit other flowers. By degrees, the stamens of the innermost whorl come to maturity; they straighten out and elongate, and their anthers with pollen exposed upon them are brought to the same level as the stigmas of the central pistils. A transference of pollen to some of these stigmas is now certain to ensue, and is rendered all the more inevitable by the outward inclination and inflection of the styles belonging to the pistils most remote from the centre which now take place, and bring the corresponding stigmas into direct contact with the pollen. But if this were all, the stigmas in the centre might get no share of pollen in the event of an absence

of insect visitors. To obviate this possibility the flower-stalk bends in a gentle curve to one side so as to bring the last-mentioned stigmas into the line of descent of the pollen when it falls from the anthers at the end of the flowering-period. The process in the Ranunculaceæ referred to only differs from that just described in trifling respects. In *Adonis vernalis* no outward inflection of the style can take place on account of its shortness, but on the other hand the stamens nearest to the ovaries curve inwards and deposit their pollen upon the adjacent stigmas. In *Anemone alpina* the anthers of the innermost whorl of stamens are the first to open, and the order of development is from that whorl outwards. Owing, however, to the fact that the styles are crowded close together in a dense tuft at that earliest stage, autogamy is not effected at once; later on the styles become bent and twisted, and some of the stigmas touch the anthers in consequence; and when in addition the pedicel undergoes inflection and causes the flower to nod, the rest of the stigmas are brought vertically under the anthers and catch the pollen which falls from them. In *Pyrola uniflora* (see fig. 308 [2]), a native of fir-woods, autogamy is brought about at the close of the flower's period of bloom by means of a marvellous co-operation of the stamen-filaments and the flower-stalks. The bud about to open (see fig. 308 [1]) and the young flower whose petals have just expanded (see figs. 308 [2] and 308 [3]) are borne on stalks which are strongly curved, and they are thus inverted and pendent. The style is vertical, with the stigma pointing downwards. The filaments are S-shaped and hold the anthers, which are of the pepper-castor type, with the two pores invariably uppermost so that the pollen does not fall out of itself or at any rate cannot come upon the stigma (fig. 308 [3]). Insects approaching from below brush first against the stigma and directly afterwards against the anthers which are in consequence upset, and besprinkle the intruders with pollen. This pollen is then carried to other flowers of *Pyrola uniflora*, where it is retained by the viscid stigmas and fertilizes the ovules. During the period of bloom two changes are effected, which though not very striking in themselves are yet of extreme importance with a view to autogamy. In the last stage of the flower the curve of the pedicel no longer amounts to a semicircle, and consequently the flower is no longer absolutely pendulous but only facing obliquely down (fig. 308 [4]); the style is no longer vertical, but with this new position of the flower points also obliquely downwards and the stigma is thus brought underneath some of the anthers. The filaments are still curved in the shape of the letter S but in the opposite direction to that held by them at the commencement of the flowering-period (*cf.* figs. 308 [3] and 308 [5]); the anthers are therefore inverted and have their pores directed downwards. The least shaking of the slender stem by the wind is now sufficient to cause a fall of pollen, and, in its present position, the viscid stigma cannot fail to get sprinkled with some particles from the shower which descends on such occasions (see figs. 308 [4] and 308 [5]).

In *Phygelius capensis*, a plant belonging to the Scrophulariaceæ of the Cape, and also cultivated elsewhere in gardens for the sake of its deep scarlet flowers, the branches of the inflorescence and the pedicels stand out nearly horizontally from

the stiff upright stem (see fig. 309 [1]). The pedicels are thickened just where they pass into the flowers and bent down so as to hold the flowers, when they are newly open, approximately at right angles to their stalks, which gives a curious appearance to the inflorescence as a whole. The flowers are protogynous, and, on the first day that they are open, the stigma can only be dusted with extraneous pollen from older flowers. The style is originally curved, so that the receptive tissue is held in front of the entrance to the floral interior where honey is abundantly secreted, and in this position it is inevitably brushed against by insects visiting the flower (fig. 309 [1],

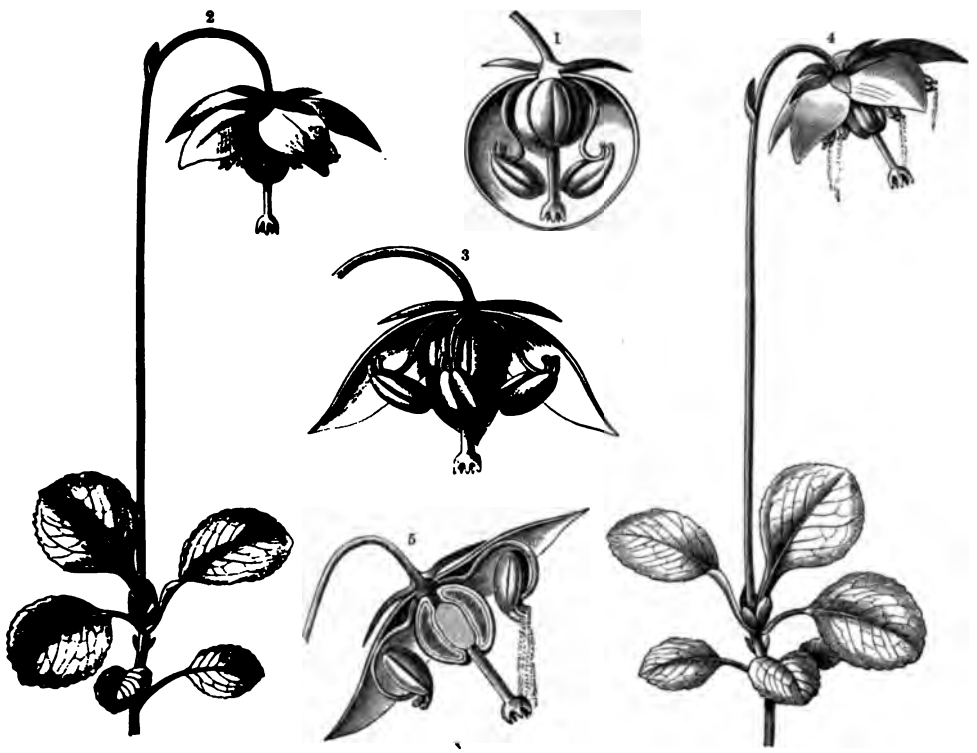

Fig. 308.—Autogamy caused by the combined inflections of pedicel and stamen-filaments: *Pyrola uniflora*.

[1] Longitudinal section through a bud about to open. [2] The whole plant with its flower in the first stage of development. [3] Flower in the first stage of development slightly magnified; the front petals are cut away. [4] The entire plant with its flower in the last stage of development. [5] Longitudinal section of a flower in the last stage of development; slightly magnified.

the right-hand flower). The next day the style straightens out, and the stigma is consequently moved away from the passage to the honey, whilst, on the other hand, the anthers open and place their pollen-coated faces exactly in the path of insects coming in search of honey (fig. 309 [1], the middle flower). On the third day the style becomes curved again and takes up the same position as it occupied on the first day. At the same time the pedicel undergoes further inflection and brings the tubular corolla nearer to the main axis of the inflorescence (fig. 309 [1], the left-hand flower). The result of these combined inflections is that the viscid stigma is brought right under the anthers at the time when they are shrivelling and catches a portion of

the crumbly pollen as it falls from them. Even if the pollen does not fall upon the stigma autogamy does not fail; for the corolla slips along the style as it drops, and is certain to touch both anthers and stigma, and to transfer to the latter the last grains of pollen adhering to the anthers (see fig. 309 [2]).

Reference has often been made in former chapters to the splendid creeper named *Cobœa scandens*, one of the Polemoniaceæ native in tropical America, but capable of thriving luxuriantly in the gardens of Central and Southern Europe, where it is used for clothing espaliers, which it covers in the height of summer with deep-purple bell-shaped flowers (see fig. 310 [1]). The anthers are borne on long filaments with hairy bases, and are situated, at the commencement of the flowering-period,

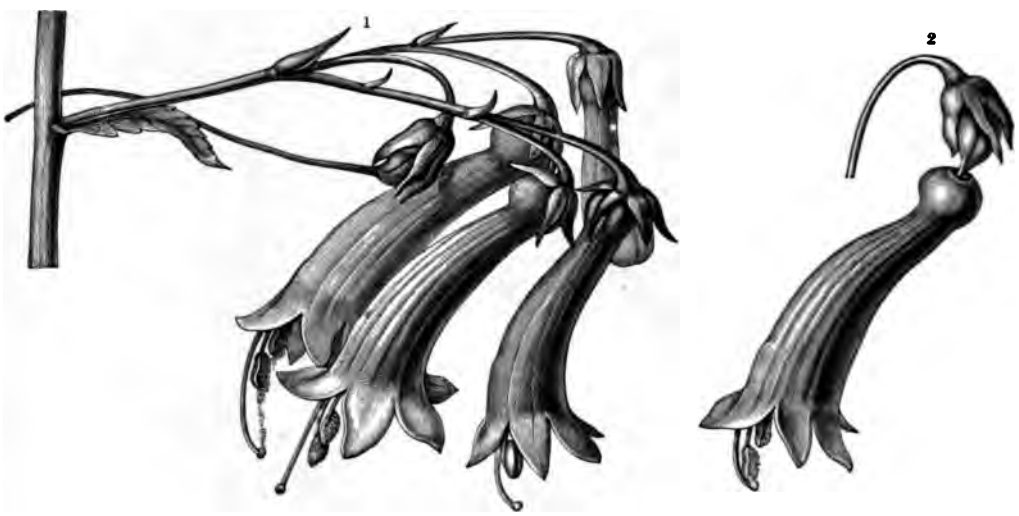

Fig. 309.—Autogamy ensuing in consequence of the inflection of the pedicel and the disarticulation of the corolla: *Phygelius capensis*.

[1] Portion of an inflorescence; the flowers borne by a horizontal branch of the inflorescence in the successive stages of development leading to autogamy (from right to left). [2] A single flower at the moment of the detachment of the corolla and the rubbing of the anthers against the stigma.

right in the mouth of the flower, where they are certain to be touched by insects which enter the flower to get the honey. The style is still short at this stage, and has its free extremity concealed under the anthers, whilst the three terminal branches of the style which bear the stigmatic tissue are closed tightly together (see fig. 310 [2]). A little later anthers and stigmas change places; the filaments elongate and twist themselves into the form of corkscrews, and the anthers then rest lower than the three style-arms, which diverge and place themselves in a position to receive pollen brought by insects from younger flowers (see fig. 310 [3]). If no insects make their appearance, and there is consequently no cross-fertilization, the pedicel undergoes inflection to the extent of about 45°, and the flower, hitherto nodding, becomes completely pendent. At the same time the style curves, and the coils of the stamen-filaments are drawn closer together. The result of all these movements is that the anthers are brought into contact with the stigmatic tissue, which is still receptive, and autogamy ensues (see fig. 310 [4]).

Allium Chamæmoly (see fig. 311 [1]) is an example of the plants, in whose flowers autogamy is effected by concurrent movements of the pedicel and the style, the former undergoing inflection, whilst the latter is inclined in the direction of the spots where the pollen has been deposited. The small white flowers are lifted but a very little way above the ground; at first they face the sky, and are half hidden amongst the long green ribbon-shaped foliage-leaves. Nevertheless, they are assiduously sought out by small insects, the honey, which is secreted in little depressions on the surface of the ovary, being in great request. During the first stage of flowering cross-pollination alone is possible; the stigma is posted in the middle of

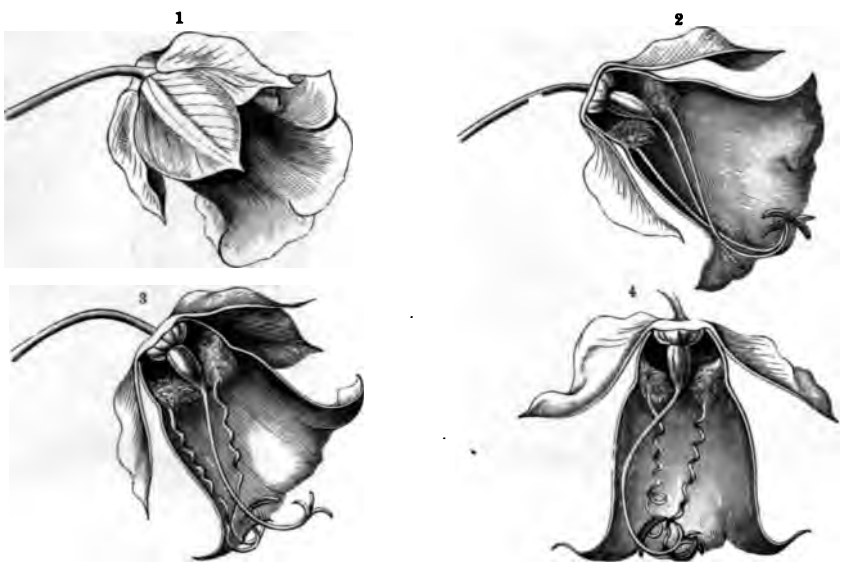

Fig. 310.—Autogamy resulting from an inflection of the pedicel accompanied by spiral torsion of the filaments: *Cobæa scandens*.

[1] Side view of a newly opened flower. 2, 3, 4 Flowers in the three successive stages of their development which lead to autogamy. All the figs. somewhat reduced.

the mouth of the flower, and its tissue is already receptive whilst the anthers are still closed and appressed to the walls of the perianth (see fig. 311 [2]). Later on all the filaments undergo inclination towards the middle of the flower; the anthers burst open, become covered all over with the pollen which issues from their loculi, and together form a yellow knob which occupies the centre of the entrance to the interior of the flower, and is brushed by all intruding insects. The stigma is at that stage hidden behind the anthers (see fig. 311 [3]), and is not touched by insects. If, for any reason whatever, insects do not visit a flower, autogamy takes place in the third stage of its development. The pedicel curves over downwards and presses the flower against the ground, and, as a consequence, the delicate white perianth-leaves and filiform stamens are displaced, and some of the pollen falls out of the anthers on to the lower perianth-leaves now resting upon the ground. The style undergoes slight lateral, *i.e.* in these circumstances downward, inclination and the final result of all these movements is that the stigma is brought into contact either with the

pollen lying on the lowest perianth-leaf or with that still sticking to one or other of the anthers (see fig. 311 [4]).

Of the plants in which autogamy is brought about by inflection of the pedicel combined with inflection or folding of the *petals*, two groups will be taken here as representing two different forms of the phenomenon. These groups consist of the Violaceæ of the *Melanium* tribe and the stemless Gentians. The manner in which the pollen is transferred to the stigma in Violets through the agency of insects has

Fig. 311.—Autogamy resulting from inflection of the pedicel combined with inclination of the style to the place where the pollen has been deposited: *Allium Chamæmoly*.

[1] Shows the aërial portions of the plant; nat. size. [2, 3, 4] Single flowers with the front perianth-leaves removed; slightly magnified. They are in the successive stages leading to autogamy.

been already described on p. 280, and illustrated in figs. 279 [1, 2, 3] on p. 279. The pollen thus deposited by insects on the slightly-projecting flap of the capitate stigma is derived, of course, from other flowers, and the result of its transference is a crossing between the flowers either of one or of two species. Autogamy is in general scarcely possible in the Violet during the first part of the flowering-period. If pollen is shaken out of the cone of anthers on to the proboscis of an insect which is in the act of dusting the front surface of the stigmatic lobe with foreign pollen, this new supply may, perhaps, be rubbed off on to the back of the stigmatic lobe as

the proboscis is withdrawn, but it does not even then come upon the receptive surface of the stigma. As regards the pollen which, though shaken out, is not carried away by the insect, but left lying underneath the cone of anthers in the trough of the spurred petal, it also does not reach the stigmatic tissue during the first stage of the flower's development, for the groove is still closed by the projecting lobe of the stigma. Towards the end of the flower's duration, however, the case is very different. The Violas of the *Melanium* tribe may be represented by the Field Pansy (*Viola arvensis*), it being the most widely-distributed species of the section. In these plants the cone of coherent anthers gradually breaks up of itself, and the pollen falls out, and fills the hinder part of the channel of the spurred petal. At the same time the lamina of this petal bends in such a manner that its trough is no longer closed by the stigmatic lobe, and the pollen is free to slip towards the mouth of the flower. The only condition now requisite is some change capable of setting the pollen in motion, and this is afforded by an inflection of the flower-stalk. Although the flower-stalk in the Field Pansy, Heart's-ease (*V. tricolor*), and other species of the *Melanium* tribe undergoes sharp inflection (see vol. i. p. 531) on clear nights, this movement has no influence in promoting autogamy at the time when the flower is in full bloom. At the last, however, it causes the mealy pollen to slip further and further down the groove in the lowest petal until it reaches the receptive stigmatic tissue.

There is a remarkable resemblance between this process and that observed to take place in those Gentians which are called by Descriptive Botanists "acaulescent" or stemless species (*Gentiana acaulis, G. angustifolia, G. Clusii*, see fig. 312). The flowers of these Gentians are of the type of "revolver-flowers" (*cf.* p. 250). The filaments are adnate to the lower part of the funnel-shaped corolla, and project in the form of five stout ridges towards the ovary, which appears as a column standing up in the middle of the flower; the ridges and the ovarian column, coming into contact with one another, divide the corolla into five tubular passages leading to the honey, which is secreted abundantly at the bottom. The anthers are a little higher than half-way up the funnel of the corolla, and are connate into a tube which surrounds the style. Each anther dehisces extrorsely by two longitudinal slits, and immediately after the flower opens the anther-tube is covered all over with pollen. Above the tube is the stigma, which is composed of two notched and lacerated white lobes. The positions of the stigmas and anthers, respectively, ensure cross-pollination through the instrumentality of the humble-bees which fly from flower to flower. If, however, unfavourable weather prevails, and the bees stop away, the pollen gradually falls from the anthers as they shrivel, and is transferred to the stigmas in the same flower through the agency of the corolla and pedicel in the following manner. As long as the flower remains upright or ascends obliquely (see figs. 312 and 312 *b*) the pollen falling from the shrinking anthers collects above the bases of the filaments, where they coalesce with the corolla, and when the corolla folds up for the night or to protect the pollen from rain, the pollen falls down between the folds, which, starting from close to the bases of the filaments, extend nearly to the

mouth of the flower. These furrows constitute, in fact, the channels through which the pollen is afterwards conducted to the stigmas. The only movements needful for the attainment of this object are the inversion of the flower, and the placing of the stigma in such a position that its fringed edges may reach to the furrows in question. Both these conditions are complied with. The inversion of the flower is brought about by a considerable elongation of the pedicel, which is very short when the flower first opens, and by its semicircular inflection at the approach of night and in wet weather (see fig. 312 [2]). The introduction of the stigmatic margins into the furrows is due to the growth of the style, which carries the stigma up into the conical cavity formed near the apex of the flower when the corolla-limb folds up.

Fig. 312.—Autogamy resulting from inflection of the pedicel combined with the folding up of the corolla.

[1] *Gentiana Clusii* showing the flower as it is when opened for the first time. [2] The same plant with its flower in the last stage of development, the corolla closed and the pedicel elongated and curved downward in a semicircle. [3] Longitudinal section through a newly-opened flower. [4] Longitudinal section through a flower which has closed for the last time.

All the furrows of the corolla-tube open into this cavity, and converge into such proximity to the axis of the flower that contact with the edges of the stigmatic lobes, which occupy the middle of the conical cavity, is inevitable. If, under these conditions, the drooping flower is shaken by drops of rain falling upon it, or by gusts of wind, the pollen slips along the smooth furrow right down to the stigma, and is caught by its fringed margins (see fig. 312 [4]). It is worthy of note that *Gentiana acaulis*, *G. angustifolia*, and *G. Clusii*—the plants to which the above description applies—grow for the most part on grassy slopes, and on the ledges of precipitous rock-faces in the Alps; thousands of flowers of these species may be seen in situations of the kind with their heads drooping in wet weather so as to lie parallel to the slope of the ground, and fruits are invariably developed from these flowers, even after long-continued rain. On the other hand, flowers growing on flat-

meadows sometimes have no opportunity of becoming nutant. In them, as might be expected, autogamy fails, and if the weather is bad, and no humble-bees are about, cross-fertilization may also be prevented; therefore it is not unusual to find many ovaries unproductive in level places of the kind.

The Pasque-flowers, *Anemone Pulsatilla* and *A. vernalis*, may be taken as representatives of the cases in which autogamy is achieved by means of an inflection of the pedicels combined with an elongation of the sepals. The flowers of these plants have very short stalks and face the sky when they first open. They remain in that position for about forty-eight hours, opening in the daytime when it is fine, and closing at night and when it rains. No drooping of the flowers is to be perceived during the first two days, and indeed such a change would scarcely be possible, considering the shortness of the stalks. The flowers are markedly protogynous. The stamens are crowded together in large numbers, and their closed anthers, grouped in the middle of the flower, resemble the grains of a head of maize. Above the anthers rises a sheaf of styles bearing mature stigmas. Insects, especially hive- and humble-bees, are attracted at this stage of floral development by the honey which is secreted by small club-shaped nectaries interspersed amongst the sepals and stamens. On entering a flower they rub against the sheaf of stigmas, even if they have not actually used it as an alighting-place, and, in the event of their bodies having been besmeared with the pollen of older flowers, a cross with some plant which may be either of the same or of another species ensues. When two days have elapsed, the aspect of affairs is altogether changed. The peduncle has become considerably longer, and the flower nods slightly when darkness sets in; the inner stamens are no longer stiff but curve outwards, whilst those anthers which are nearest to the styles have undergone dehiscence and offer their pollen for dispersion. The sepals, which are concave towards the middle of the flower, have elongated somewhat to protect the pollen. Insects now come in quest of pollen as well as honey, and are certain to get dusted with a quantity of it which they may then transport to other flowers. When a flower closes in the evening, pollen from the anthers of the reflexed stamens is invariably affixed to the inner surface of the superincumbent sepals. At this stage, too, pollen is liable to be shaken out of the anthers of the longest stamens, and this falls, in the case of a nodding flower, on to the central stigmas of the fascicle of styles. Two days later, again, the condition of the flower is as follows:—The stalk is from ten to twenty times as long as it was, and the flower is nutant in the daytime as well as by night. The stamens have all relaxed from their rigidity; the filaments are curved outwards, and the anthers are open. The sepals have more than doubled their original length, and the pollen affixed to their inner surfaces has consequently been raised to the level of the stigmas. In addition, the form of the three inner sepals has changed; the concave inner face is now convex, and the external surface is concave. The result of these changes is that the stigmas at the periphery of the fascicle now receive their share from the elongated sepals, which are appressed to them and yield up to their receptive tissue the pollen sticking to their inner surfaces.

The processes which lead to autogamy in the Water Avens (*Geum rivale*), the Raspberry (*Rubus Idæus*) and some other Rosaceæ allied to these are even more complicated than those above described. Thus, for example, the flowers of *Geum rivale*, on the day that they open, face laterally and have their stalks horizontal; the filaments are short, and the anthers are all closed, while the stigmas which project in a tuft 2 mm. beyond the anthers are already mature. At this stage insects may occasion cross-fertilization, but autogamy is not yet possible. Subsequently, the filaments lengthen and the anthers of the longest stamens open and come into contact with some of the stigmas at the periphery of the bundle of styles. The pedicel is now curved and the flower nods; consequently, the pollen which falls from the anthers above, when they shrivel, is forthwith received by the outer stigmas of the fascicle of styles, that is to say, by those of the outer stigmas which appertain to the upper half of the flower. The pollen which falls from the anthers of the under half of the flower when they dry up, is caught, on the other hand, by the petals on that side of the flower, and is afterwards transferred, by means of an elongation of these petals, to the stigmas of the adjacent reflexed styles. A couple of days later the pedicel is curved into a semicircle, and the flower hangs down with its mouth towards the ground. By this time the anthers of the shorter stamens are open; the whole flower has become loosened, and the fascicle of styles resembles a sheaf of corn. All the styles, including those in the middle, become twisted and reflexed to the extent necessary to bring the stigmas underneath the most recently opened anthers, and when these anthers shrivel and the pollen is forced out, it falls upon the central stigmas, which hitherto have not been furnished with any. Thus, in this case we have (1) the inflection of the pedicels, (2) the elongation of the petals, (3) the elongation of the stamens, and (4) the inflection of the styles—all co-operating towards the same end, namely, that in the event of no insects visiting a flower all the stigmas may receive pollen from the anthers developed in the flower itself.

The foregoing descriptions, though extremely brief and cursory, give a general idea of the many kinds of contrivances whereby autogamy, as well as heterogamy, is promoted in hermaphrodite flowers. It is evident from them that any mechanism which leads to autogamy has full scope for its operation only if cross-pollination has not previously been effected. Again and again we have found that certain processes only take place in the event of a flower being unvisited by insects through whose agency cross-fertilization would have been brought about. In this connection we have also the remarkable phenomenon that many flowers adapted to cross-fertilization by insects do not open at all when there is no chance of their being visited by the agents in question. In the mountainous districts of the temperate zones it often happens that rainy weather sets in just at the time when the flowers are about to open, and that it lasts for weeks. Humble- and hive-bees, butterflies, and flies retire to their hiding-places, and for a considerable time cease to pay any visits to flowers. The growth of the plants is not, however, arrested during this period, and even in the flowers themselves development quietly progresses if the

temperature be not too low. The stigmatic tissue becomes receptive; the anthers attain to maturity, dehisce and liberate their pollen notwithstanding that no ray of sunshine penetrates the clouds and that rain falls continuously. In such circumstances the mouth of the flower is not opened; autogamy takes place in the closed flower, and all the adjustments evolved with the object of ensuring cross-fertilization are ineffectual. This is the case, for instance, in the following:—*Alsine rubra, Anagallis phœnicea, Arabis cærulea, Azalea procumbens, Calandrinia compressa, Centunculus minimus, Drosera longifolia, Gagea lutea, Gentiana campestris, G. glacialis, G. prostrata, Hypecoum pendulum, Hypericum humifusum, Lepidium sativum, Montia fontana, Oxalis corniculata, O. stricta, Polycarpon tetraphyllum, Portulaca oleracea, Sagina saxatilis, Silene noctiflora, Sisyrinchium anceps, Spergula arvensis, Stellera Passerina, Veronica alpina, V. bellidioides* and *V. Chamædrys*—plants which grow in widely different habitats, but which all have the common property that their flowers open for but a short period, if at all. In plants with long-lived flowers it is of not uncommon occurrence for autogamy to be accomplished during a spell of wet weather, and for the petals to open subsequently all the same, and so afford the possibility of the remains of the pollen being carried away by insects. This phenomenon has often been observed, for example, in *Rhododendron hirsutum*, the Bog-bean (*Menyanthes trifoliata*), and the Greater Dodder (*Cuscuta Europæa*).

There is also the case of such plants as *Alisma natans, Illecebrum verticillatum, Limosella aquatica, Peplis Portula* and *Subularia aquatica*, which live in pools or on the banks of ponds where the level of the water is variable. If the buds of these plants are submerged at the time when they are about to open, they do not unfold, and autogamy takes place in the closed flowers under water. It must be observed that the water does not penetrate into the air-filled interior of the flowers, so that we have here the curious phenomenon that the transference of pollen to the stigma, though accomplished under water, is yet a case of pollination in the medium of the air.

An allied phenomenon is exhibited by some of the Knotweeds (*Polygonum Hydropiper, P. minus*, and *P. mite*). Isolated plants of any of these species, in which all the flowering branches are exposed to the sunshine, and are both visible and accessible to insects, unfold all their flowers; but, if hundreds of one species are crowded close together, only a limited number of the flowers open their perianths. The flowers growing on the upright branches alone of such crowded plants unclose, and receive insects' visits, whilst those which grow on the under, procumbent branches, and are consequently concealed and not easily reached by insects, remain shut. Nevertheless autogamy is effected with obvious success in these also.

Plants of the kind just alluded to form a transition to those which normally produce two kinds of flowers, viz.: some which open and are adapted to cross-fertilization through insect-agency, and some which remain closed and exhibit autogamy with great regularity. The latter have received the name of *cleistogamic* (κλειστος=that can be closed, γάμος, marriage) flowers, and amongst them may be dis-

tinguished a series of very wonderful forms. A common characteristic of them all is the stunted development or complete abortion of petals which would otherwise attract insects by their scent, colour, or honey. The only function of the petals is that of an envelope under cover of which ovules and stigmas, anthers and pollen, attain maturity and are able to enter into combination with one another. In many cases there is no trace of a corolla to be seen; green sepals alone are developed into a floral envelope, and they are kept fast closed and cover the stamens and pistil in the form of a hollow cone. Thus, for instance, *Aremonia agrimonioides*, a plant growing abundantly in the forests of Carniola, has cleistogamous flowers about a millimetre in diameter, in which stamens and sepals spring from the edge of the excavated disc, whilst petals are entirely absent. In other cases, though petals exist, they remain small and of a greenish-white tint. Precisely those parts of the corolla which in open flowers are most conspicuous in form and coloration are here abortive. Thus, in the cleistogamous flowers of several species of Violet, the spurred petal, which in the open flower is the most striking, is scarcely recognizable; its lamina is oval in outline, and is rolled into a hollow cone covering the anthers and stigma. The anthers in most cleistogamous flowers are so situated that when the pollen is ripe and issues from the loculi it comes immediately into contact with the stigma. Sometimes, it is true, there is a tiny interval between the pollen adherent to the anther-lobes and the stigma, but in that case tubes are put forth by the pollen-cells in the direction of the stigma, and these tubes lay themselves upon the papillæ on the stigmatic surface and thence pursue their way to the ovules. In the cleistogamous flowers of the Henbit Dead-nettle (*Lamium amplexicaule*) it has even been observed that the anthers do not open, but that, nevertheless, pollen-tubes emerge from the pollen-cells, perforate the walls of the anther and grow in the direction of the stigma until they reach it. If a cleistogamous flower of this kind is examined after autogamy has been accomplished within it, one might at first sight think the anthers and stigmas were adnate to one another, so firm is the union of the pollen-tubes with the stigma.

As has been already said, all species of plants which produce cleistogamous flowers also develop other open ones. For the most part these latter possess very striking forms, scents, and colours, and are adapted to receive the visits of insects and to undergo cross-fertilization through their agency. It is interesting to note, however, that these open flowers possess none of the contrivances for effecting autogamy in the event of a dearth of insects. From these observations we are justified in supposing that we have here a sort of division of labour, inasmuch as the functions, usually discharged by one form of hermaphrodite flower alone, are here divided between two kinds of flower—both also hermaphrodite—viz., cross-fertilization is assigned to those that open, self-fertilization to those that remain closed.

Amongst Grasses, Rushes, Scirpuses, and other plants of the kind, which produce dust-like pollen in their hermaphrodite flowers, only a few species are known to possess cleistogamous flowers. The oldest established example is that of *Oryza*

clandestina, a widely-distributed bog-grass allied to the Rice-plant. The panicles of this *Oryza* include chiefly flowers which remain closed and are adapted to autogamy; they develop only on their very highest branches a few flowers which open and may be cross-pollinated by the agency of the wind. On the other hand, the number of species possessing cleistogamous flowers to be found amongst plants with adhesive pollen, and liable to be crossed by insect agency, is very large. Numbers of tropical and sub-tropical Asclepiadaceæ, Malpighiaceæ, Papilionaceæ, and Orchidaceæ afford instructive examples of this phenomenon. The splendid colours of the open flowers in these plants attract insects, and if the flowers are visited cross-pollination is rendered inevitable by the various kinds of apparatus for pressing, sprinkling, or shooting the pollen upon the insects with which the flowers are furnished; but if in spite of allurements no insects arrive, the stigmas are not besmeared with pollen at all, and these great open flowers wither without forming fruit. It then comes to the turn of the cleistogamous flowers. They are developed in the axils of special leaves as small, greenish, bud-like structures, which are destitute of means for alluring insects, but are none the less sure on this account to produce ripe fruit and fertile seeds. There is, besides, in temperate zones, no lack of plants in which the same phenomenon may be observed. A host of Bell-flowers, Rock-roses, Balsams, Polygalaceæ, Oxalidaceæ, and Scrophulariaceæ (e.g. *Campanula, Specularia, Helianthemum, Impatiens, Polygala, Oxalis, Linaria*) and, in particular, the Violas of the *Nominium* and *Dischidium* sections, exhibit the same difference in the functions assigned to their two kinds of flowers. The beautiful *Viola mirabilis* has scented flowers stored with honey, which unfold great violet petals in the spring. If these blossoms are visited by hive- or humble-bees they are cross-fertilized; but many are not thus visited, and their fate is then to wither without effecting that process of autogamy which has been described (p. 387) as taking place in the species of Violet belonging to the *Melanium* section. In the summer, however, special branches of the same individual plant bring forth small green flower-buds which do not open, but nevertheless produce soon afterwards large ripe capsules full of seeds. This phenomenon, in apparent contradiction to the ordinary idea of the result of the flowering process, did not escape the attention of the Botanists of the eighteenth century, and they named this species of Violet, in which the majority of the large open blossoms fail to produce fruit whilst the closed bud-like flowers are invariably productive, *Viola mirabilis*, or the Wonderful Violet.

In *Viola mirabilis* and in all its allied species, called "caulescent" in the language of descriptive Botany, the cleistogamous flowers are developed on special shoots, and these shoots are either erect or else prostrate in long zigzags. This is also the case in several species of the Wood-sorrel genus (*Oxalis*) and in *Aremonia agrimonioides*. A few Papilionaceæ (e.g. *Vicia amphicarpa*) and Cruciferæ (e.g. *Cardamine chenopodiifolia*) are known too, whose cleistogamous flowers spring from underground runners or stalks, whilst the open flowers are borne upon aërial shoots. In several Violets of the kind called by descriptive Botanists "acaulescent", such as *Viola collina* and *V. sepincola*, the cleistogamous flowers develop likewise

underground, their stalks springing from special shoots of the rootstock. In all these cases the two kinds of flowers are always borne on the same plant, though on different branch systems; there are, however, also instances, such as the Yellow Balsam (*Impatiens Noli-tangere*), where the open flowers are developed on different individuals from those which produce the closed ones. To be accurate we should say that the statement in each case expresses the general rule for the plants in question, for instances of transition are by no means uncommon. Thus, for example, individual plants of the Yellow Balsam do occur in which open flowers with large corollas, half-open flowers with stunted corollas, and small cleistogamous flowers stand side by side; and, again, on the zigzag runners of the Sand Violet (*Viola arenaria*) flowers with large expanded petals have often been seen growing in company with the cleistogamous flowers. The same remark applies as regards the time at which cleistogamous flowers make their appearance. In the majority of cases they are not developed until the open flowers have withered and disappeared, but in *Cardamine chenopodiifolia* it has been observed that the subterranean cleistogamous flowers are produced earlier than those which are borne on above-ground stems and unfold their petals to the air.

In former times it was asserted that plants exist which never bear any but cleistogamous flowers. Thus the Toad-rush (*Juncus bufonius*) was stated to produce cleistogamous flowers only. Later investigations have, however, established the fact that this plant possesses two kinds of flowers—viz. terminal flowers with three stamens which are cleistogamous, and lateral flowers with six stamens which open, like those of other Rushes, under the warmth of the noonday sun. It was also supposed that the African species of *Salvia*, to which the name of *Salvia cleistogama* was given, produced cleistogamous flowers only, but after repeated sowings plants have been obtained with flowers which opened. Anyone who has only seen the Yellow Balsam growing on the heaps of detritus brought down by the mountain-streams in the upland valleys of the Tyrol might think that this plant also was an instance of a species producing cleistogamous flowers only; for in those localities open flowers are not found on this species. But if seeds from these cleistogamous flowers are sown in good vegetable mould, in a partially shaded spot in a garden, a few individuals with large open yellow flowers spring up, as a general rule, even after a single sowing. There is a species of Violet named *Viola sepincola* which grows deep in the shade of the woods clothing the hills at the foot of the Solstein chain in the Innthal district. I saw it there for the first time about the middle of May, and it was then covered with an abundance of ripe fruit. In following years I looked for flowers of this plant early in the spring, as soon as the snow had melted, but found that not a single individual had developed open flowers with expanded petals on erect above-ground stalks. On the other hand, there were a number of cleistogamous flowers concealed under the fallen leaves and partially buried in the earth, so that it looked very much as if the species produced no other kind of blossom. But plants subsequently reared in a part of my garden which was exposed to the sun's rays during some hours of each day developed, in the next

year but one after their being sown, in addition to cleistogamous flowers, beautiful scented blossoms of a violet colour which were borne on erect stalks and in due time unfolded their petals.

This result throws some light on the nature of the stimulus which causes the formation of the flowers in question. No open, aërial flowers were produced by *Viola sepincola* so long as it grew in the cool shade of a dense wood, but when transferred to open ground, accessible to sunlight, such flowers were developed. One can hardly err in ascribing to the sun's rays a very important influence in stimulating plants to the inception of flowering shoots, especially such as bear blossoms possessing bright-coloured petals. Indirectly, however, this advantage accrues to the plants in question that, living as they do in the deep shade, where no bees would, in any case, visit them, even if they had open flowers, they can confine their constructive energy to the inception and development of cleistogamous flowers and save themselves the trouble of producing open flowers adapted to cross-pollination (but useless in the place in question). If the spot where the Violet grows becomes exposed to the sunlight through the trees shading it being blown down or felled, humble- and hive-bees make their appearance in search of honey, and, buzzing from flower to flower, cross one with another. In such circumstances the open, sweet-scented Violet blossoms are in request, and the same plant-individual, which for years in the dark shade has developed none but cleistogamous flowers, is now stimulated by the sun's rays into producing flowers with expanded petals.

A similar instance is afforded by the Henbit Dead-nettle (*Lamium amplexicaule*), which grows on cultivated ground—in kitchen-gardens, vineyards, and amongst crops. This plant bears two kinds of flowers, viz. some with purple corollas 15 mm. in length, which keep the entrance leading to their honey wide open, and, secondly, cleistogamous flowers with abortive corollas and small green calices, which remain closed. As is the case with many other annual weeds, Dead-nettle plants which have germinated late in the season maintain their vitality through the winter and into the following spring, and accordingly they may be seen at all seasons flourishing, fresh and green, in situations such as are mentioned above. Flowers, too, are initiated and developed by them at all seasons of the year, but it is interesting to note that only in the warm summer, when flower-seeking insects are about, are the beautiful purple corollas of this plant to be seen; in the late autumn and early spring, when it is cool, and there are no flower-seeking insects, this Dead-nettle is able to do without the luxury of corollas, which are the means of alluring insects, and as a fact only cleistogamous flowers make their appearance at those seasons. It must not, of course, be imagined that the plant exercises an intelligent discretion of its own when it abandons the development of corollas. The connection between this effect and the aforesaid conditions is indirect, and we must conceive that the nature of the stimulus which results in the inception of flower-buds is different, when a plant is subject to the influence of the short days and low temperature of late autumn and early spring, from what it is under the conditions prevailing on warm summer days.

Amongst the contrivances mentioned in the last chapter as being adapted to bring about cross-fertilization at the commencement of a flower's period of bloom, was the production of heterostyled flowers (see pp. 302 and 312). It was pointed out (p. 316) that in heterostyled plants the very first, or last (as the case may be), of all the flowers of a particular species are, in consequence of the dichogamy which prevails, fated to be crossed with flowers of another species, or, in other words, to undergo hybridization, and that, according to experience, this crossing is often effective. Considering the results obtained in the cases of other plants with hermaphrodite flowers, one would expect to meet with some provision for the timely fulfilment of autogamy in heterostyled species as well, *i.e.* that in the event of no insects visiting a plant of the kind, the stigmas should at the proper moment be dusted with pollen from the anthers in the same flower. This expectation has been, in fact, confirmed; all the investigations directed to this question having resulted in showing that a process of autogamy takes place also in heterostyled flowers, but is always confined to one only of the forms which together constitute the species. In one section of the heterostyled species, including, for example, those which belong to the genera *Gentiana*, *Menyanthes*, and *Thesium*, the short-styled flowers are adapted to autogamy, whilst in others, such as the heterostyled species of *Mertensia* and *Pulmonaria*, autogamy takes place in the long-styled flowers. In *Primula longiflora* and *P. minima* it is the short-styled flowers which have their stigmas dusted with pollen from their own anthers, whilst in *Primula Auricula*, and *P. glutinosa* it is the long-styled flowers which thus accomplish self-fertilization. All these variations are exactly adjusted with reference to the other arrangements for promoting autogamy in the flowers in which they are exhibited.

One contrivance which deserves mention here is the disparity in the size and conspicuousness of the floral envelopes in the two forms of flowers of the same species. In *Primula longiflora* and *P. minima* the long-styled flowers, and in *Primula Auricula* and *P. glutinosa* the short-styled flowers have a larger and more striking limb to their corollas than the other forms in each case. It may be taken to be a general rule that the flowers adapted to cross-fertilization, in which no autogamy takes place, are larger than those in which the accomplishment of autogamy is assured. This phenomenon has been explained by the circumstance that flowers destined to be crossed with others require to be more plentifully equipped with the means of attracting insects than those which are certain to undergo fertilization even if no insects visit them.

The means whereby autogamy is achieved in species with heterostyled flowers are in the main the same as they are where the flowers are not heterostyled. In some cases the stamens, or the petals with pollen affixed to their surfaces, elongate sufficiently to enable the stigmas to come into contact with them: in others the same result is attained by an inclination or an inflection of filaments or style; in a third series the stigma is dragged through the ring of anthers when the corolla falls off, or the petals by opening and closing effect the transference of the pollen from the anthers to the stigma; and lastly, in some instances, the pedicels undergo elongation

and inflection, which result in bringing the stigma underneath the anthers, so that when the latter shrivel their pollen must fall upon the receptive tissue. Of the host of observations relating to this matter, we can here only select a few to serve as examples, and the most suitable for our purpose will be the Primulas, to which reference has already been frequently made, viz. *Primula Auricula*, *P. glutinosa*, *P. longiflora*, and *P. minima*.

The corolla in the short-styled flowers of *Primula Auricula* has a comparatively large expanded limb, the surface of which is slightly concave; the five stamens are adnate to the contracted throat of the corolla, where the tube passes into the limb, and the anthers form, at that part of the flower, a ring through the middle of which insects must penetrate in order to enter the floral interior. The style is short, and the spherical stigma at the top of it stands at a level corresponding to only a third of the length of the corolla-tube. At the time when the dehiscence of the anthers takes place, the flowers are in a nodding or horizontal position. In these circumstances no pollen can reach the stigma, and, unless visited by insects, the flower remains unpollinated until it fades, nor does the fall of the corolla operate as a means of conveying pollen from its own anthers to the receptive tissue. It is quite different with the long-styled flowers of the species in question. The limb of the corolla is rather smaller, and is hollowed into the shape of a basin; the five stamens are adnate to the lowest third of the tube, and their anthers stand at the same height as does the stigma in a short-styled flower. The style is long, and the stigma may be seen in the middle of the flower's throat. In other respects there is no difference worth mentioning between the two forms. The stigmas of the long-styled flowers are liable to be dusted with pollen brought by insects from the anthers stationed in the throats of short-styled flowers. Whether this occurs or not, the receptive tissue under any circumstances gets covered with pollen when the corolla becomes detached and falls off, for the stigma is then dragged through the ring of anthers in the corolla-tube, and is certain to remove some of the pollen which still adheres in more or less abundance to them.

Altogether different is the process of autogamy as manifested in *Primula longiflora*. In this case the corolla of a long-styled flower has a shorter tube and larger limb than that of a short-styled flower. The anthers are situated in the throat just behind the mouth of the corolla-tube. The style is long and projects far beyond the throat, whilst the stigma is held considerably above, that is to say, in front of the ring of anthers. The flowers are either horizontal or else ascend obliquely, and neither of these positions admits of pollen being deposited by the anthers upon the stigma. As in this species the corolla does not drop but persists even when withered, no autogamy takes place in the long-styled flowers when the plant is growing wild. On the other hand, every insect which enters the flower must necessarily touch the stigma, stationed where it is in front of the passage, and cross-fertilization then ensues. The short-styled flowers have a longer tube and smaller limb to the corolla. Their anthers, unlike those of many other Primulas, are situated in the throat close beneath the corolla-limb in the same position as in the long-styled flowers; but the

style does not project outside the throat, and its stigma rests only just above the tips of the anthers. Under these conditions cross-pollination is as likely to be brought about through insect-agency as it is in the case of the long-styled flowers; but in addition autogamy takes place towards the end of the period of bloom. The manner in which the latter is effected is as follows:—During the period of the flower's bloom the corolla-tube grows some millimetres in length until finally the ring of anthers, which are adnate to the throat of the corolla, is brought up to the same level as the stigma. The stigma then stands in the centre of the ring and receives an abundant supply of pollen from the adjacent anthers.

In *Primula minima* (see figs. 288 [1] and 288 [2], p. 302) the heterostyled flowers are erect and maintain this position unaltered till the corolla withers. The limb of the corolla in the long-styled form (see fig. 288 [1]) is larger than it is in the short-styled form. The anthers in the long-styled flower are inserted on the lower part of the tube; the style projects above the ring of anthers and the stigma rests somewhere in the uppermost third of the tube. On entering a flower an insect would first come against the stigma, and would then probably dust it with foreign pollen. Autogamy scarcely ever takes place. In the wild state of the plant the corolla withers without falling off; only in rare instances does it happen that the corolla becomes detached from the receptacle, and is carried away by the wind. On such an occasion the stigma might touch the ring of anthers and get covered with pollen. Self-fertilization is, on the other hand, all the more carefully ensured in the short-styled flowers. Here the anthers are attached to the highest third of the corolla-tube, and the stigma capping the short style rests below the ring of anthers. When the flower's period of bloom is nearly at an end both the corolla-tube and the anthers begin to wither and contract, with the result that the pollen falls from the anthers down the tube, and is caught upon the stigma.

Thus, autogamy is effected in the long-styled flowers of *Primula Auricula* and *P. glutinosa* by the stigma being dragged through the ring of anthers as the corolla falls off, in the short-styled flowers of *Primula longiflora* by the elongation of the corolla-tube and elevation of the anthers to the level of the stigma, and in the short-styled flowers of *Primula minima* by the anthers shrivelling and letting their pollen fall. The fact of the occurrence amongst Primulas alone of three kinds of contrivance for promoting autogamy gives us some idea of the immense variety which prevails in this respect amongst heterostyled plants in general. The impossibility of entering here into the further details of this subject is the less to be regretted, seeing that to a great extent such an account would involve a repetition of facts which have already been stated.

The number of species possessing heterostyled flowers is far larger than was formerly supposed. The list of such species known at the present day includes members of the following families: Boraginaceæ, Caprifoliaceæ, Caryophyllaceæ, Colchicaceæ, Crassulaceæ, Ericaceæ, Gentianaceæ, Globulariaceæ, Iridaceæ, Linaceæ, Lythraceæ, Onagraceæ, Oxalidaceæ, Papaveraceæ, Plantaginaceæ, Plumbaginaceæ, Polygonaceæ, Primulaceæ, Rubiaceæ, Santalaceæ, Solanaceæ, and Valerianaceæ, and

it is probable that more thorough investigation will result in the addition of many more instances, especially amongst tropical plants. In most cases the species of one genus produce only two forms of flowers; but there are also genera—such as *Linum* and *Oxalis*—in which some of the species develop long-, mid-, and short-styled flowers, others long- and short-styled forms, and others again none but flowers with styles of equal length. The determination of the point as to whether heterostylism exists or not in a particular case is, in many species, attended with some difficulty, owing to the stamen-filaments increasing in length during the period of the flower's bloom in both the long-styled and the short-styled flowers—a circumstance which greatly complicates the relations subsisting between the two forms in respect of the lengths of their different parts. There is also some danger of mistaking for heterostyled species a class of forms which do not in reality come under that category. In the species alluded to, a proportion of the individual plants produce apparently hermaphrodite flowers, with ovaries, styles, and stigmas which can be clearly identified as such, but which nevertheless are not capable of undergoing fertilization.

The results of the investigations into the subject of autogamy recorded in this chapter may be summed up as follows. In plants whose flowers are hermaphrodite, but neither cleistogamous nor heterostyled, both cross- and self-fertilization occur in one and the same flower at different epochs; in plants with cleistogamous flowers a division of labour is established between two kinds of hermaphrodite flowers, of which the one form opens and is adapted to heterogamy, whilst the other remains closed and can only result in autogamy; and, lastly, in heterostyled plants, each species includes two or three different forms of individual, varying in respect of the structure of the flowers, which in the one case aim at cross-fertilization, and in another especially at autogamy.

In view of the detailed consideration which the methods for promoting autogamy in various plants has received in the foregoing pages, it may not be without interest to allude here briefly to the relative prevalence of this mode of pollination in certain Floras. During the passage of the present edition of this work through the press, a notable addition to our knowledge of Floral Biology has been made by E. Loew (*Blütenbiologische Floristik*), in the form of a treatise wherein are summarized the vast number of observations upon flowers and their relations to insects, &c., so far as the Floras of Europe and Greenland are concerned, that have been published in one place and another during the last ten years. This tabulating of observations has enabled the author to make many interesting comparisons between the Floras of various regions, and, supported by statistics, to exhibit the relative prevalence of types adapted to this or that method of pollination. Though many of the results do but confirm views already the common property of Biologists, they have an altogether special value from the manner in which they have been obtained.

As regards autogamy, it appears from statistics that it shows an increase in high Alpine forms as compared with plants from a lower level. The accompanying

table, taken from Loew, contrasts alpine and sub-alpine plants in regard to the relative prevalence of autogamy:—

(I.) Of 130 entomophilous plants in *sub-alpine* regions—
35 species = 26·9% are rarely or never autogamous.
86 species = 66·1% are autogamous as well as heterogamous.
9 species = 6·9% are invariably or usually autogamous.
99·9%

(II.) Of 133 entomophilous plants in *high alpine* regions—
35 species = 26·3% are rarely or never autogamous.
78 species = 58·6% are autogamous as well as heterogamous.
20 species = 15·0% are invariably or usually autogamous.
99·9%

Thus we see that 20 high alpine species show pronounced autogamy as compared with 9 sub-alpine forms.

In the mountain Flora of Scandinavia the prevalence of autogamy is even more marked.

(III.) Of 74 species from the Dovrefjeld—
12 species = 16·2% are rarely or never autogamous.
40 species = 54·0% are autogamous as well as heterogamous.
22 species = 29·7% are usually autogamous.
99·9%

As compared with the high alpine plants (table II.) we note a diminution of 10% in those which are always heterogamous, and an increase in those usually autogamous of some 15%.

In plants whose distribution is restricted to the Arctic regions, the number of autogamous plants is in the majority.

(IV.) Of 45 species of purely Arctic plants—
0 species = 0·0% are almost exclusively heterogamous.
14 species = 31·1% are autogamous as well as heterogamous.
26 species = 57·8% are usually autogamous.
5 species = 11·1% are doubtful.
100%

Precisely what factors in their environment have led to this increased prevalence of autogamy in high alpine and far northern species is at present not certainly determined. A lack or comparative rarity of insect-visitors on the one hand, or unfavourable climatic conditions on the other, might either of them well lead to such a condition. Regarding the alleged paucity of insects in the Alps, one so well qualified to speak as Hermann Müller says[1]:—"I have not been able to convince myself that alpine flowers are, on the whole, less frequently visited and crossed by insects than are those of the plain". Nor does Loew, with the statistics before him, dissent from Müller's opinion. So also with regard to the northern types, concerning which the view is widely spread that their preponderating autogamy is connected

[1] *Alpenblumen*, p. 547.

with the paucity of insects. Loew is of the opinion that the insects there are adequate for the work they have to do, *i.e.* are sufficiently numerous for the maintenance of the species of plants which depend upon their visits.

Putting aside the visits, and proceeding to consider the climatic conditions, we are on much surer ground. Both on the mountains and in the far north the period of vegetation is a short one, and the shortness of the summer, combined with the broken character of the weather, which is common to the Alps and Arctic regions during that period, can hardly fail to promote autogamy amongst the plants growing in those regions. Such as have flowers that can pollinate themselves spontaneously will be more sure of ripening their seeds before the brief summer ends than will such the flowers of which must wait for insects. In the foregoing pages several instances have been described in which autogamy is promoted by the closing of the flowers. By these movements the pollen is mechanically transferred to the stigmas. It may well be that by the considerable increase which must accrue in these closing movements, owing to the frequency of unfavourable weather in alpine and arctic regions, a further condition favouring autogamy is obtained.

FERTILIZATION AND FORMATION OF FRUIT IN PHANEROGAMS.

Pollination, or the dusting of the stigma with pollen, is only the prelude to the phenomenon known as *Fertilization*. It is important to distinguish clearly between these two events, especially as the term "fertilization" is frequently used by authors when they really mean "pollination"—indeed, this substitution is almost inevitable in many cases, the custom being what it is. Fertilization can only occur in Phanerogams after previous pollination, though pollination does not invariably connote a subsequent fertilization. Thus, cases are known in which flowers, pollinated by insects at the proper time, do not produce fruit, and others in which the pollen of the same flower falls upon the stigmas with a like failure of result. In other words, both cross-pollination and autogamy may be without result.

It must be explained, to prevent misunderstanding, that the older accounts of this lack of result attending pollination should be received with caution. Formerly, judgment was passed rather hastily as to the results of pollination in hermaphrodite flowers, as it seemed obvious that the sexual elements must, unavoidably, come together. If no production of fruit took place in a really hermaphrodite flower, it was assumed that pollination was without result, and no precautions were taken to demonstrate that pollination had actually occurred. Thus it happened that certain plants were regarded as sterile, although this sterility had only been observed upon isolated specimens growing in gardens. In many cases the flowers of the plants in question were strongly protogynous, *i.e.* at the time when the stigmas should have been pollinated there was no pollen, there being no plants growing near with flowers in a more advanced stage. Similarly, such flowers cannot be autogamous, as the two sets of organs are never at maturity simultaneously. They are marked out for cross-pollination. When for any reason this does not take place, fertilization

and fruiting obviously cannot occur. It is instances of this kind that are adduced by the older botanical writers to prove that the hermaphrodite flowers of certain species are infertile.

Plants have also been regarded as sterile from the fact that the particular insects necessary for the transfer of their pollen were absent from the locality in which the observations were made. Thus, *Paederota Ageria*, a plant not infrequently found in rocky crannies in the Southern Alps, and cultivated in large quantity in the Innsbruck Botanic Garden, was always found to be sterile in the last-mentioned locality, although it flowered profusely. The flowers of the plant require insects to pollinate them, as the relations of the parts are such that autogamy cannot occur. Since the particular insects which visit it in its own habitat are absent from the Botanic Garden, the plant is infertile from lack of pollination. In its own home in the Southern Tyrol and Krain, where these insects are present, it ripens an abundance of fruits. The same is the case with several introduced plants which have become partially wild. The Sweet Flag (*Acorus Calamus*), truly indigenous to Eastern Asia, has spadices of densely-crowded, hermaphrodite flowers. The individual flowers are strongly protogynous, and when the anthers open, the stigmas of the same flower are already faded. Autogamy is consequently excluded. The opening of the flowers is from below upwards, and when the anthers of the lowest flowers are discharging their pollen the stigmas of the uppermost flowers are still capable of pollination. Could the pollen pass from the lower to the upper flowers, geitonogamy would take place, but this is only possible through the agency of insects, as the pollen is adhesive. In Europe, where the plant is not originally indigenous, this never happens, as the insects which visit it are absent; consequently, with us, *Acorus* is always sterile. But further east, where it is indigenous, its flowers are pollinated by insects, and it produces its fruit in spikes of red berries. The Day Lily (*Hemerocallis fulva*) has ephemeral flowers which open in the morning in summer-time between 6 and 7 o'clock, and close between 8 and 9 in the evening. Its flowers are protogynous for a very short time. For half an hour before the opening of the flower the mature stigma projects from the tip of the perianth. Simultaneously with the folding back of the perianth, the anthers liberate their adhesive pollen. The style being longer than the stamens, its stigma is not automatically pollinated. For pollination insect visits are necessary. Honey is secreted at the base of the tube of the perianth, which is 2 cm. long. The entrance to this honey is so narrow that only a very delicate proboscis can gain access. Beetles, flies, bees, and other short-tongued insects cannot get it, nor would they be of any use for pollination if they could. The whole flower seems adapted for the visits of some large butterfly with a long, thin proboscis, but curiously enough the flowers of *Hemerocallis fulva* are never visited by butterflies in Europe. As autogamy is excluded, the flowers remain unpollinated, and are sterile. Neither in gardens, where it is much cultivated, nor in its semi-wild state does the Day Lily ever fruit with us. It is more than probable that *Hemerocallis* is visited, in Northern Asia and Japan, where it is truly indigenous, by some butterfly absent from Europe.

It has been already mentioned (p. 156) that the flowers of the American Yuccas are pollinated by small moths, unknown in Europe, and that these flowers set no fruit with us. Also, that several species of Catchfly, indigenous to the Southern and Eastern Alps, though robbed of their honey by humble-bees, are but seldom pollinated and fruitful (p. 239).

Lastly, many cultivated plants, depending on insects for fertilization, flower in gardens earlier or later than in their wild surroundings. In nature, their period of flowering coincides with the time of flying of certain insects; in gardens—even when the insects in question occur—the flowers may be too early or too late for the insect season. From what has been said above, it will appear that sterility in many cases is only apparent, and is due merely to the lack of the normal and necessary conditions for bringing about pollination.

In other cases it may happen that although the stigmas are pollinated, the pollen cells are abortive and incapable of producing pollen-tubes. This condition of the pollen obtains most frequently in gardens amongst plants on rich, well-manured soil, artificially-produced hybrids, and plants whose stamens are partly converted into petals. At the same time it must not be supposed that by any means all plants which show a "doubling" produce bad pollen; for instance, many double Roses produce pollen which is used by gardeners for artificial pollination with good results. Still, in the majority of such plants abortive pollen is the rule, pollen which is non-effective on the stigma.

In nature, especially in places where many plants flower at the same time, as on the borders of a wood, in meadows and heaths, it is unavoidable that the pollen of various species should be deposited on one and the same stigma. Insects certainly show a preference for a single species for considerable periods, particularly when this species is flowering in quantity on a confined space; still, anyone who closely observes insects visiting flowers can easily convince himself that the flowers visited are changed from time to time. A bee which has just dusted itself with pollen in the flower of a Winter Aconite (*Eranthis*) will fly across to visit a bush of *Salix daphnoides*, and as it passes a plant of *Daphne Mezereum* it will suck its honey; a moment later it will swoop down to the flowers of *Crocus vernus* in the meadow near by, and then fly on to the Sweet Violet (*Viola odorata*). On the stigma of the last-mentioned plant will be found the pollen of all or several of the just-visited flowers, on the Crocus that of the Willow, and so on. The case is similar with wind-pollinated flowers. I have found the pollen of the Spruce Fir (*Abies excelsa*) and of Dog's Mercury (*Mercurialis perennis*), both brought by the wind on to the stigmas of the Herb Paris (*Paris quadrifolia*); and on another occasion the stigmas of *Gagea lutea* were so thickly dusted with the pollen of *Alnus viridis* that there would have been no room for any pollen more.

That the pollen of the Willow will fertilize the Crocus, that of Dog's Mercury the Herb Paris, or that of the Alder the Gagea is *a priori* improbable. Only such changes take place in the pollen as always occur when it is placed on a moist substratum; all further stages in its development are arrested. The commencing

pollen-tubes, sometimes found, though in some cases they penetrate the tissues of the stigma, do not fertilize the ovules. It is another question whether or no this "foreign" pollen is entirely without effect, whether it does not possibly influence the stigmatic tissue so that less foreign pollen, arriving later on the same stigma and developing pollen-tubes, is affected. But this subject can only be dealt with later on; here it suffices to state that all pollen falling on a stigma is not necessarily suitable, and that the stigma has, in a manner of speaking, to make a selection.

It is very difficult to say what conditions come into play in this choice of pollen. Experimental inquiry into this matter has not been wanting, but its results tell us little as to the fundamental processes at work. By it we ascertain little more than whether this or that artificial pollination leads to a production of seeds or not. Thus in one case no seed will be formed, in another a few, and in a third case an abundant crop. The sources of error in this class of experiment are considerable, nor do the results by any means always harmonize. Thus, in experiments of my own as to the fertility of certain Catchflies when pollinated from allied forms, no result would be obtained in one year, whilst in the following year their repetition led to the production of a certain number of seeds. Other observers have had the same experience; and it would seem that whatever care be exercised, absolute reliance cannot be placed on the result—especially where it is a negative one. Caution must be used, therefore, in generalizing from such experiments, especially in cases where their number is limited. In the main, the general results are very instructive, and must not remain unnoticed here in so far as they relate to the connection between fertilization and the origin of new species.

These results may be shortly summarized as follows. When the pollen of one species is placed on the stigma of another species, pollen-tubes capable of fertilizing the ovules are developed only when the two species belong to the same genus or to the same natural family of plants. Families and genera are conceptions devised by Botanists, and although their limitations are to some extent arbitrary or dependent on the personal equation of individual observers, in the main there is little difference of opinion as to these limitations in the case, at any rate, of families. How far new discoveries may lead to a revision of their present limits must remain undecided, but, of families as at present laid down, we may say that crossings of pollen between species of two different families (orders) is without result, whilst between species of two different genera very rarely is seed produced.

The crossing of species of the same genus results, in most cases, in fertilization, and eventually in the production of hybrids. It is certainly remarkable, in this connection, that external similarity between the two species crossed has little bearing on the result or absence of result. One of the commonest of naturally-produced hybrids is one which owes its origin to the union of *Primula glutinosa* with *Primula minima*, two species very dissimilar in the form of their foliage and flowers. On the other hand, hybrids of the very similar Cowslip and Bardfield Oxlip (*Primula officinalis* [*veris*] and *Primula elatior*) are but rarely met with in nature, whilst artificial pollinations between them only occasionally lead to any result.

If ripe pollen from the male flowers of a plant be placed on the mature stigmas of female flowers of the same species, the result may be regarded as certain. This holds good equally for monœcious and dicœcious plants, and for such also as have apparently hermaphrodite flowers in which one or other set of sexual organs is more or less abortive, so that the flowers in question are to all intents and purposes unisexual.

It has been shown that for plants with true, non-heterostyled, hermaphrodite flowers, a transfer of ripe pollen from the anthers of one flower to the mature stigma of another, belonging to the same species, constantly leads to fertilization. In those cases only in which the stamens are of unequal lengths is pollination attended with unequal results, according as the pollen has been taken from the longer or shorter stamens.

The behaviour of plants with hermaphrodite heterostyled flowers is peculiar. Pollen from the anthers of a short-styled flower applied to the stigma of a long-styled flower, or from a long-styled flower applied to the stigma of a short-styled flower, gives the best result. The other possible combinations, *i.e.* pollen from long-styled or short-styled flowers applied to the stigmas of the same class of flower give indifferent results, and frequently none at all. Experiments have shown in the case of the Loosestrife (*Lythrum Salicaria*), which, as we have seen (p. 303), possesses long-, mid-, and short-styled flowers, that crossings between stamens and styles of the *same* length ("legitimate unions") are fruitful, whilst all other crossings ("illegitimate unions") are either quite sterile or followed by only a sparing production of seed.

It has been demonstrated that the pollen-cells of heterostyled flowers vary both in size and colour according to the length of stamen (or height of anther or corolla) producing them. Thus, in the Loosestrife, the dry pollen-cells of the long stamens are green, and 30–38 μ long and 20–26 μ broad; those of stamens of the middle length are yellow and 23–26 μ long and 13–16 μ broad; those of the short stamens are also yellow, but 20–25 μ long and 11–13 μ broad ($\mu = \frac{1}{1000}$ millimetre). In the Cowslip (*Primula officinalis* [=*veris*]) the pollen-cells, produced by anthers at the mouth of the corolla-tube (and destined for a long style), have a diameter of 30 μ, those arising from anthers low down the tube (and destined for a short style), a diameter of only 20 μ. The explanation offered by Delpino of this difference in size—that, other things being equal, pollen-tubes which have to traverse a greater distance to reach the ovules require a more ample supply of reserve-materials than those which have less far to penetrate—sounds plausible, but the problem is probably a rather more complex one than appears at first sight. As a general result of experiments upon heterostyled plants we may say that the most copious production of good seed results from a pollination of stigmas with pollen from stamens of similar height.

As to the result of *autogamy* (self-pollination) in ordinary hermaphrodite flowers, it would appear, in all cases where the stamens are of unequal heights, that the pollen has a dissimilar effect according as it comes from a longer or shorter stamen. If pollen, which *would not unaided reach the stigma* of the same flower, be artificially transferred to that stigma, the product is usually very small. If, however, *pollen which would ultimately reach the stigma* of the same flower be artificially

transferred thither a good crop of seed results. Artificially produced autogamy in hermaphrodite flowers, in which the stamens are all of one length, is generally productive, nor does it appear to matter whether the pollen used for pollination be taken from the first stamen to open or the last. The number of species in which artificial autogamy is unfruitful is extremely small. *Crambe tatarica, Draba repens, Lilium bulbiferum, Lysimachia nummularia,* and a few Orchids and Papilionaceæ may serve as examples, though even in these cases it is quite possible that some source of error, such as was mentioned at the commencement of this chapter, has been overlooked.

We may now proceed to discuss what is known as the *prepotency of foreign pollen over own pollen.* The term "foreign" is used of pollen upon a stigma which has been brought from another flower of the same or of some other species; "own" pollen, on the other hand, is applied to such as has originated in one of the anthers of the *same* flower. These terms are employed for the sake of brevity. If one examines a flower of *Corydalis* early in the morning of the day on which that flower will become accessible to insects, one finds that the anthers have already dehisced, and that the stigma is covered with own pollen. The stigma, lying between the two spoon-shaped petals, is regularly embedded in pollen. But as yet the stigma is immature and unreceptive, so that the absence of any interaction between pollen and stigma at this stage is intelligible. When insects come in due course, a portion of this pollen will be removed (*cf.* p. 266). Should the insects have visited *Corydalis*-flowers previously, they will leave some of the foreign pollen with which they are dusted upon the stigma at the moment when they remove some of the own pollen. The stigma is now in contact with both own and foreign pollen, nor will additional insect-visits materially alter this state of affairs. In due time the stigma becomes receptive and exerts a selective action upon the pollen. Though the process, as it takes place here, cannot be followed step by step, still we are justified in assuming, on the results of many experiments of artificial pollination, that the foreign pollen receives the preference. It has been shown for *Corydalis cava* that the flowers are absolutely barren to their own pollen, only slightly fertile to pollen from another flower on the same plant, and only thoroughly fertile when impregnated with pollen from a different plant. For other species, however, e.g. *Corydalis capnoides, fabacea,* and *ochroleuca,* it has been shown that the plants are fertile to their own pollen, so that if no insect-visitors come, the flowers do not remain sterile.

These results show how fallacious it would be to make the condition obtaining in *Corydalis cava* the basis of any far-reaching generalization, such as that autogamy is prevented, and without result. In point of fact, autogamy is highly productive in most species of *Corydalis,* and occurs, in such plants as are unvisited by insects, in the closed flower in a manner recalling that form of autogamy known as cleistogamy (*cf.* p. 391). That foreign pollen is prepotent in *Corydalis capnoides, fabacea, ochroleuca,* &c., when both foreign and own pollen are present on the stigma together, is neither asserted nor denied, though, in view of all the circumstances, it seems probable.

In agreement with *Corydalis* stand numerous species of *Fumaria*, and a great number of Papilionaceæ, especially those whose flowers possess a piston-apparatus (*cf.* p. 260). *Pisum* and *Ervum*, *Lotus* and *Melilotus*, the various species of *Trifolium*, almost all of them, when unvisited by insects, ripen seed, only a few species here and there being infertile when dependent upon their own resources. Thus we may say that when the stigma has to choose between own and foreign pollen, the latter probably gets the preference, though, when own pollen alone is present, it is adequate for fertility.

A similar condition obtains amongst the Scabiouses (*Scabiosa*) also. Their flowers are hermaphrodite and protandrous, and united into heads. At the time when the anthers dehisce, the pollen remains hanging to the stigmas, although these are not as yet actually receptive. For the time being, this pollen is without effect. By the visits of insects a portion of this pollen is removed and replaced by foreign pollen, which is ultimately, on the maturing of the stigmas, probably preferred to the own pollen. In the absence of insects, however, the flowers are undoubtedly fertile to their own pollen.

Likewise, in many Labiates (e.g. *Leonurus heterophyllus*) and Scrophulariaceæ (e.g. *Linaria littoralis* and *minor*), has essentially the same state of affairs been shown to exist. One more instance only need be described, that of a Catchfly (*Silene noctiflora*). This plant opens its flowers at about seven in the evening. If, however, the flowers be opened artificially a little earlier, at about six p.m., it is found that all the anthers have already dehisced, and that the delicate stigmatic papillæ are already dusted with the pollen from the five short stamens. Thus, already in the bud, autogamy has taken place in a manner not unlike cleistogamy. As the flowers open in spite of this, it can only be on the chance of crepuscular or nocturnal moths visiting them and bringing foreign pollen. The flowers of this Catchfly are not very eagerly sought after by insects, still now and again a *Plusia* or other owlet moth may be seen flitting from flower to flower, sucking honey and bringing and taking pollen. Thus, again, a selection of pollen by the stigma probably occurs with preference for the foreign; otherwise, why need these flowers open at all since the stigmas are already coated in the bud with own pollen? In the absence of insects the own pollen will be potent and lead to seed-production. In wet, cold weather also, when the flowers do not open at all, the ovules ripen into seeds, no doubt impregnated by their own pollen. In all the cases enumerated the behaviour is essentially the same, in the early stages of flowering the opportunity is given for cross-pollination by insects, but, wanting this, autogamy or self-pollination ensues.

We may now pass on to speak of the *germination of the pollen-grain* upon the stigma and of the development of the pollen-tube. The pollen is at this stage influenced by the receptive stigma. There would appear to be a taking up of fluid matter by the grain, though its exact nature has not been accurately determined. Since, however, pollen-grains germinate readily in a 3-per-cent sugar-solution, it is extremely probable that sugar is an important component of this stigmatic fluid.

The first demonstrable stage in the production of the pollen-tube is the pushing

out of the delicate inner coat of the grain in the form of a tube through the thin places in the extine. The structure and distribution of these thin spots has been already described (p. 102); it need only be added that a tube may be pushed out at each or any of them. When pollen is artificially cultivated in a prepared sugar-solution several tubes arise simultaneously from different spots, but, in nature, on the stigma, the production of a single tube is the rule. The tube which contains the whole of the contents of the pollen-grain (spermatoplasm) forsakes the extine, which remains behind as a dead shell. Very soon after its appearance through one of these holes in the extine, the pollen-tube comes to have a considerable diameter, often approaching that of the grain in size. The tube now elongates, growing always at the expense of the stigma. Its mode of growth is similar to that of a fungal hypha, and its relation to the stigmatic tissues resembles that of the hypha of a parasitic fungus to its host. Like the parasite, it is able to penetrate the subjacent tissue and to make its way through it for long distances.

This penetration by the pollen-tube is certainly amongst the most remarkable properties of flowering plants. The object of these wanderings is to reach and fertilize the ovules contained—in Angiosperms—in the closed chamber of the ovary. Whether the stigma be sessile upon the ovary or situated upon a style, the distance to be traversed is considerable, and, in a very large number of cases, the way leads through closed tissues. As the pollen-tubes travel as a rule by definite rows of cells or tracks, we may assume that these latter are in some way specialized for their conduction; still it is very puzzling to understand exactly in what manner these cells become thus qualified. In all likelihood the pollen-tubes are attracted by certain substances secreted by the tissues, which they have to traverse in order to reach the ovules. Of these sugar seems to be the most important, and by a continuous secretion of this (and possibly other substances), the tubes are led on to the ovules. Casual allusion has already been made to the fact that the motile spermatozoids of Cryptogams swim through the water to the archegonia (amphigonia) in response to a somewhat similar stimulus (p. 68).

Investigations into the course followed by the pollen-tubes in passing from the stigma to the ovules show that it varies in different cases. Simplest, and perhaps typical of what was formerly supposed to be the route universally followed, is the case of the Martagon Lily (*Lilium Martagon, cf.* fig. 313 [1]). If the columnar style of this plant be cut longitudinally one sees that it is penetrated by a canal which narrows below towards the ovary, but widens out into a funnel at the stigma, where it opens by a tri-radiate slit. The lips of this aperture bear numerous papillæ; to these the pollen-grains become attached and here commence to form their tubes. The tips of the pollen-tubes curve down into the funnel and grow along the cells which line the style-canal (fig. 313 [1]). Passing down this canal, which is at this time more or less mucilaginous, the pollen-tubes are led ultimately to the cavity of the ovary in which are contained the ovules.

Very different is the mode of travelling of the tubes in Grasses, of which *Avena elatior* (fig. 313 [2]) may be taken as type. Upon the spherical ovary of this plant

two delicate feathery stigmas are inserted (*cf.* fig. 231, p. 139). The shaft of each of these stigmas consists of elongated, succulent, colourless cells, whilst the barbs of the feather are extremely delicate and filamentous in character, and have the upper extremities of the cells of which they are composed continued as little papillæ (fig. 313 [2]). Neither in the main axis nor in the branches of the stigma are canals present. The cells fit edge to edge, and the pollen-tubes must bore a way for themselves in order to traverse the tissues in this case. The pollen-grains are attached to the

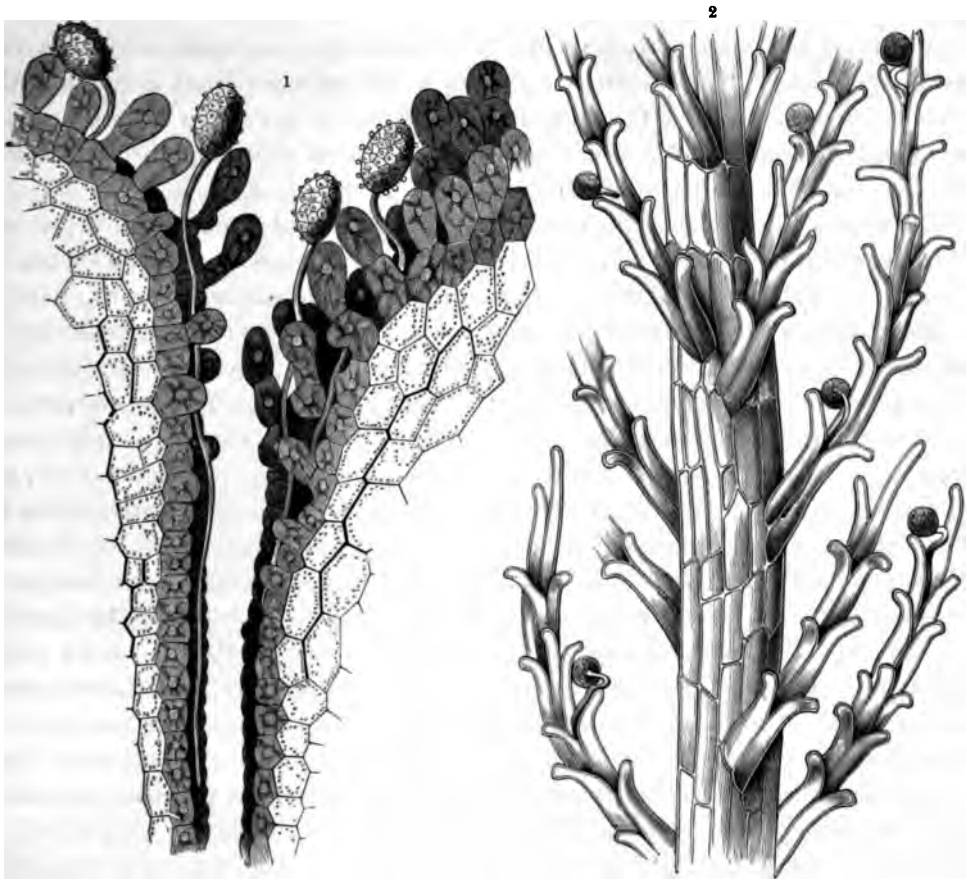

Fig. 313.—Development of Pollen-tubes.

[1] Longitudinal section of the stigma and upper portion of the style of *Lilium Martagon*. The pollen-grains present on the stigmatic papillæ are sending their tubes down the mucilaginous cells of the style-canal (after Dodel-Port); ×110.
[2] Portion of the feathery stigma of *Avena elatior*. Pollen-grains are attached to the papillæ, and their tubes may be seen boring in between the cells of the stigmatic branches; × 170.

papillæ, and as the little pollen-tubes are produced, these latter bend round so as to grow down along the inner face of the papilla. To do this they often execute very complicated curves, or they may grow spirally round the papillæ. Having reached the angle at the base of a papilla, they bore themselves a passage between the superficial cells and grow henceforward down to the ovary in an intercellular channel of their own making.

In the Grasses not only is no pre-existing canal present, but the cells between

which the pollen-tube penetrates show no demonstrable difference from their neighbours. In this respect the Grasses differ from the very large number of plants which, although they do not possess an open style-canal as in *Lilium Martagon*, have a loose axial string of mucilaginous tissue in their styles through which the pollen-tubes readily penetrate. Examples of this condition are the Solanaceæ and Scrophulariaceæ. In other cases the conducting tissue is not differentiated from its surroundings, so that the whole of the substance of the style and stigma serves for the conduction of the pollen-tubes, as in *Cistus*, *Helianthemum*, and Orchids.

A curious condition prevailing in the Cactuses has been observed in the frequently mentioned *Cereus*. Here, although a narrow style-canal is present, the pollen-tubes prefer to make their way to the ovary embedded in the tissue surrounding the canal. From this it would appear that it is of advantage for the pollen-tubes to travel thus inclosed by other tissues.

Different again is the course followed by the pollen-tubes in the Malvaceæ and in many Caryophyllaceæ. The stigmas here are in some degree like those of Grasses. As there, so here, the superficial cells are produced into long, thin-walled papillæ; to these papillæ the pollen-grains become attached by the agency of insects. The pollen-tube as it develops from the grain at once perforates the wall of a stigmatic papilla and continues its growth in the cell-cavity. The course now followed is remarkable. In the Corn Cockle (*Agrostemma Githago*) the pollen-tube often zigzags from one side of the cavity of the stigmatic papilla to the other, not infrequently taking first of all the wrong direction and bending up towards the tip of the papilla, and then bending completely round again. Having reached the base of the papilla, the tube bores through into the conducting tissue in the interior of the style, but in its further course down to the ovary grows solely between the cells, not in them. It sometimes happens that more than one tube arises from a single pollen-grain; the accessory ones, however, are for purposes of firmer attachment, and though they occasionally enter a stigmatic papilla do not continue their growth down the tissue of the style. One functional pollen-tube only is produced from each pollen-grain. In the Malvaceæ (e.g. *Malva sylvestris*) the pollen-tube entirely fills a stigmatic papilla, broadening out at the base. Ultimately the contents of the tube escape from their membrane and travel down the style in an elongated mass, destitute of wall, like the plasmodium of a Myxomycete.

Whatever be the manner of its travelling, whether with or without a wall of its own, the aim of the protoplasm of the pollen-grain is to reach one of the ovules in the ovary. Having entered the cavity of the ovary, a pollen-tube shapes a course for an ovule. The particular portion of the ovule aimed at—in the vast majority of flowering plants—is the *micropyle* (*cf.* vol. i. p. 644), the little receptive spot at which the coats of the ovule are discontinuous, and at which access to the embryo-sac (wherein is contained the *egg-cell*) can be gained. Only comparatively rarely is the micropyle situated immediately below the point at which the pollen-tube must enter the ovary, as represented, for instance, in fig. 208[3], p. 74. Sometimes the micropyle is directed towards the side wall of

the ovary, sometimes towards the central column, as in the Star of Bethlehem (*Ornithogalum*, figs. 315[3, 4, 5]); whilst frequently the ovule is inverted so that the micropyle faces the base of the ovary (*cf.* fig. 211[8], p. 79). Since, in the majority of plants, several ovules are contained in a single ovary and each is fertilized by a separate pollen-tube, we find a number of tubes traversing the style, and, on their entering the cavity of the ovary, diverging to the several ovules. One would expect now to find this portion of the route to be followed by the pollen-tubes well

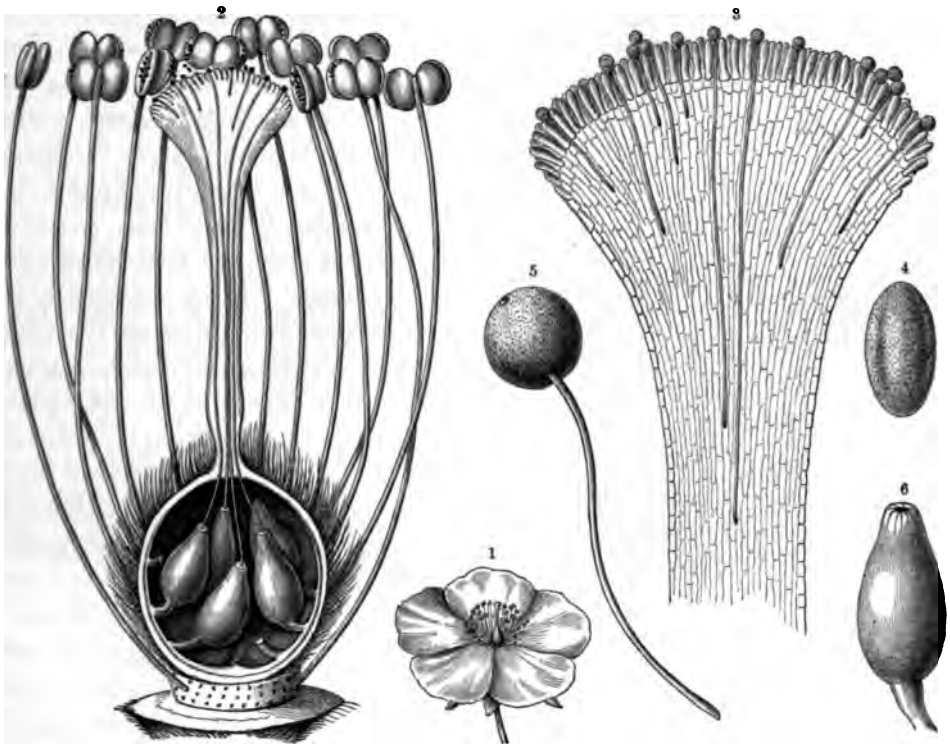

Fig. 314.—The course of the pollen-tubes in a Rock-rose (*Helianthemum marifolium*).

[1] A single flower, natural size. [2] A flower, stripped of its sepals and petals, showing stigma and style and ovary in longitudinal section; the pollen-tubes are seen passing down the style to the ovary and there going one to each ovule (the tubes are indicated erroneously as going direct to the micropyles; actually they follow a more devious course, first down the inside wall of the ovary and then up to the micropyles); ×22. [3] Stigma and upper portion of style in longitudinal section; shows pollen-grains attached to the stigmatic papillæ and tubes penetrating the tissues; × 55. [4] A dry pollen-grain; × 300. [5] A moistened pollen-grain developing its tube; × 300. [6] An ovule—which in this plant is of rather unusual form, the micropyle being at the end of the ovule distant from the point of attachment; ×50.

indicated, either mechanically as by furrows and grooves, or by lines of secretory and nutrient cells leading to the micropyle. This, however, seems to be very rarely the case. As a rule such obvious guiding mechanisms are wanting. The pollen-tubes creep along the inner wall of the ovary to the places where the ovules are borne and then turn up and enter the micropyles, one pollen-tube to each ovule. The adjacent figure 314[2] shows for a Rock-rose (*Helianthemum*) the whole course of the tubes from the stigma to the micropyles. As the tubes enter the cavity of the ovary they diverge and pass one to each ovule. A slight error, however, has crept into the figure in question in that the tubes are represented as passing *direct*

to the micropyles. In point of fact they follow a more roundabout course, creeping along the ovary wall, and then up the individual ovules to the micropyle.

It has been stated above that the pollen-tube enters the ovule *at the micropyle* in the vast majority of flowering plants. But this is not universally the case, as recent investigations have proved. In several of the trees belonging to the group of the Amentaceæ the pollen-tube follows an altogether different course. This was first established for the case of *Casuarina*, a curious switch-plant indigenous to Australia and certain parts of Eastern Asia. A small portion of a branch of this tree is shown in fig. 69 [5] (vol. i. p. 299). *Casuarina* is wind-pollinated, the flowers being unisexual, though both male and female flowers are borne on the same individual. The pollen-grains germinate in due course on the stigma, and their tubes traverse the tissues of the style. The tubes do not, however, enter the cavity of the ovary, but continue their growth immersed in the tissues of the ovary. They thus make their way to the points of insertion of the ovules, where they enter them, and at once travel to the base or *chalaza*. From the base of the ovule the pollen-tube penetrates towards the apex of the ovule, reaching the egg-cell from below, not from above as in cases in which the pollen-tube entered the ovule by the micropyle. This type of fertilization has been termed *chalazogamic* in contradistinction to the more usual micropylar or *porogamic* method. Quite lately a renewed examination of many common trees belonging to the Amentaceous group has shown that in several of them also fertilization is chalazogamic. This is the case in the Hazel (*Corylus*) and Hornbeam (*Carpinus*, fig. 314 A), belonging to the Corylaceæ, as also in the Birch (*Betula*) and Alder (*Alnus*, fig. 314 B), belonging to the Betulaceæ. In the Hazel and Hornbeam the pollen-tube, after reaching the base of the ovule, passes straight up to the egg-cell in the embryo-sac (*cf.* fig. 314A, *p.t.*) in a manner similar to *Casuarina*, but in the Birch and Alder its course is

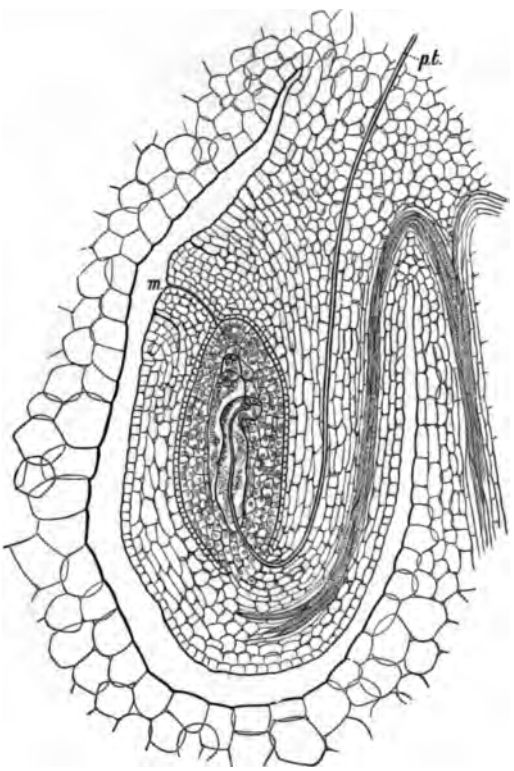

Fig. 314 A.—Chalazogamic fertilization in the Hornbeam (*Carpinus Betulus*).

The drawing shows a longitudinal section of an ovule almost filling the cavity of the ovary. The micropyle (*m*) and the two integuments are shown above the apex of the nucellus (in whose cells the nuclei are indicated). Within the nucellus three embryo-sacs are represented; a pollen-tube (*p.t.*), passing down into the substance of the ovule from the placenta, follows the course of the raphe and at the base of the nucellus (chalaza) bends sharply round and enters one of the embryo-sacs; its tip penetrates to the egg-cell at the apex of the embryo-sac. Much enlarged (from a drawing by Mrs. Macdonald).

not so direct. Here it passes by the embryo-sac on one side and then turns sharply down again, reaching the egg-cell from the same direction as it would have done had it entered by the micropyle (*cf.* fig. 314 B, *p.t.*). It is interesting to note that in many nearly allied Amentaceæ, as in the Cupuliferæ, which includes the Oak (*Quercus*), Beech (*Fagus*), and Chestnut (*Castanea*), fertilization is by the micropyle.

The following table indicates the method of fertilization as at present known in the various families comprehended in the group Amentaceæ:—

AMENTACEÆ.	*Mode of fertilization.*
1. Betulaceæ.	
Betula, *Alnus*	Chalazogamic.
2. Corylaceæ.	
Hazel (*Corylus*), Hornbeam (*Carpinus*)	Chalazogamic.
Hop Hornbeam (*Ostrya*)	Not ascertained.
3. Cupuliferæ.	
Oak (*Quercus*), Beech (*Fagus*), Chestnut (*Castanea*)	Porogamic.
4. Juglandaceæ.	
Walnut (*Juglans*)	Porogamic.
Carya, *Ptero-carya*, &c.	Not ascertained.
5. Myricaceæ.	
Sweet Gale (*Myrica*)	Porogamic.
6. Casuarineæ	
Casuarina...	Chalazogamic.
7. Salicineæ.	
Willow (*Salix*), Poplar (*Populus*)	Porogamic.

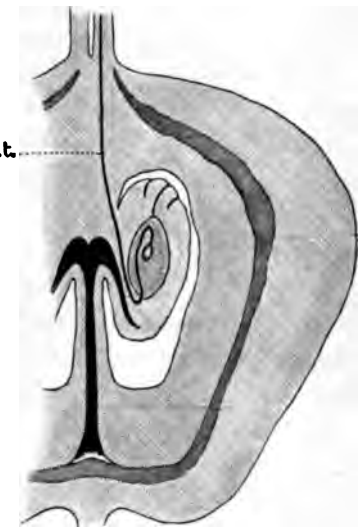

Fig. 314 B.—Chalazogamic fertilization in the Alder (*Alnus glutinosa*). Diagrammatic.

The drawing shows one half of a longitudinal section of the ovary. The wall of the ovary is thick, and has a hardened middle layer (shaded dark). At the top is the base of the style, from which the pollen-tube (*p.t.*) can be traced passing straight on through the substance of the ovary to the ovule. Entering the ovule by its point of attachment to the placenta the pollen-tube bends sharply upwards (at the chalaza) into the nucellus. It now passes by the small oval embryo-sac on the inner side, and when below the micropyle turns sharply down to the apex of the embryo-sac. The vascular supply of the ovules, which forms a column in the placenta, is shaded dark. Considerably enlarged (from a drawing by Mrs. Macdonald).

Many experiments have been made from time to time with a view to explaining the phenomena attendant on the wandering of the pollen-tube from the stigma to the micropyle. It has been shown that the pollen-tube is extremely sensitive to various external conditions, and that by appropriately varying these the direction followed by the tube in its growth may be controlled. Pollen-tubes are especially sensitive towards sugar-solutions, and bend out of their course towards the sugar. They also tend to grow away from the air, and show a preference for spaces saturated with aqueous vapour to such as are less humid. Of all the conditions which affect a pollen-tube, most conspicuous is the attraction which sugar exerts upon it. Various portions of the pistil exert a similar chemical stimulus on pollen-tubes, very marked being the action of the micropyle in this respect. A few of the experiments demonstrating this attractive property of stigma and ovules may be briefly described. If a fresh mature stigma be cut off and laid on a plate of gelatine, and

the gelatine in its immediate neighbourhood be dusted over with pollen-grains of the same plant, in the course of a few hours, as the pollen-tubes are developed, it will be found that they converge upon the stigma in an unmistakable manner. Pollen-tubes, even at so considerable a distance from the stigma as seventy times their own diameter, have been observed to be influenced in this way. Similar results obtain when sections of a style are employed instead of a stigma, but the attraction is not so strong. Isolated ovules laid on the gelatine exert a very marked attraction upon pollen-tubes. In one case as many as forty pollen-tubes were counted converging upon the micropyle of an ovule of *Scilla patula*. Ripe ovules ready to be fertilized exert the strongest attraction, though younger and as yet immature ovules are not without influence.

Noteworthy is the fact that an ovule is found to attract not only pollen-tubes from pollen of the same species, but of others far removed from it in point of affinity. Thus the pollen-tubes of *Scilla patula* (a Monocotyledon) were found to be attracted by the ovules of *Diervilla rosea* and *Ranunculus acer* (Dicotyledons), tubes of *Primula sinensis* by the ovules of *Antirrhinum majus* and *Digitalis grandiflora*, those of *Hesperis matronalis* by ovules of *Lonicera Periclymenum*, &c. In these experiments these strange pollen-tubes were not only attracted towards the micropyle, but actually in a few cases penetrated it. Still, no suggestion is made that anything of the nature of fertilization could be accomplished by these foreign pollen-tubes.

Nor is this attraction limited to pollen-tubes. The delicate hyphæ of several mould-fungi are similarly attracted, as also, when the surface on which the ovule rested was moistened, was that common micro-organism of decomposition, *Bacterium Termo*.

Thus it appears that substances are present in the stigma, style, and ovules, which exert a chemical attraction upon pollen-tubes, gradually leading them to the micropyle. Though it has not been possible to determine in all cases what these substances are, it is extremely probable that they are of a sugary nature. In the case of plants with chalazogamic fertilization, in which the pollen-tube, as we have seen, never enters the cavity of the ovary, it would be of interest to ascertain if the micropyle is destitute of attraction for pollen-tubes.

As stated, the attraction exerted by a given ovule or portion of a pistil is not limited to pollen-tubes of the same species, but seems common to pollen-tubes in general, and indeed to fungal hyphæ and the like. Thus it happens that instances are recorded in which fungal spores fell on the stigma, and germinating there, sent their hyphæ down the style to the ovary like pollen-tubes. And so with foreign pollen. Though it is often stated that the pollination of the stigmas of a plant A with pollen from B (a plant not allied to A) is *without result*, what is actually indicated is that no seed has been ripened by the pistil thus pollinated. Experiment has shown that, just as the pollen-tubes of one plant may be attracted towards the micropyle of an ovule of a plant of entirely different family, so pollen will germinate on the stigma of a similarly remote plant and form tubes which penetrate

considerable distances down the style, though they perish eventually. Still even should these foreign pollen-tubes actually get access to the micropyle, a fertilization of the egg-cell by the foreign spermatoplasm would be impossible, owing to the inability of the sexual protoplasm to combine outside a very narrow range of affinity. We have already seen that many plants can be fertilized either by pollen from another flower of the same species, or, wanting this, by their own pollen.

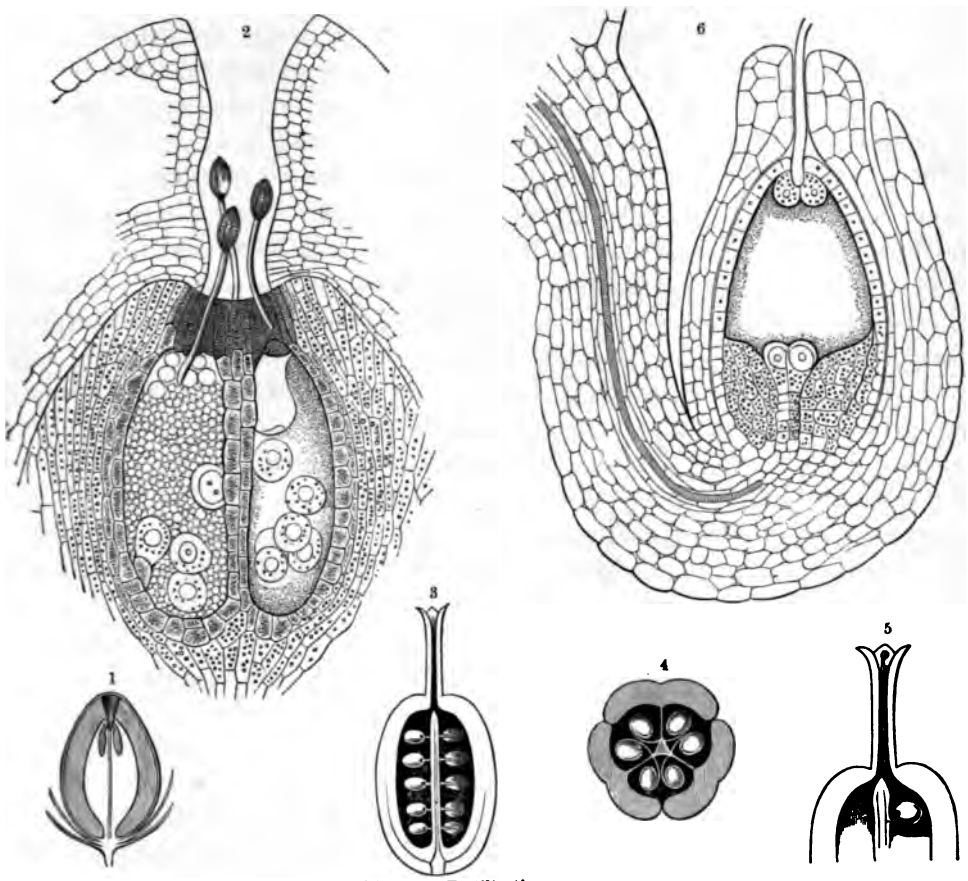

Fig. 315.—Fertilization.

[1] Longitudinal section through the ovule of *Ephedra* (a Gymnosperm); ×3. [2] Apical portion of a longitudinal section of the nucellus of *Ephedra*, showing the pollen-grains in the excavated apex with their pollen-tubes; ×100. [3] Longitudinal section through the ovary of *Ornithogalum nutans*; × 2. [4] Transverse section of the same ovary; × 3. [5] Longitudinal section through stigma, style, and upper portion of ovary of *Ornithogalum* showing a pollen-grain on the stigma with its pollen-tube passing down the style-canal to the micropyle of an ovule; × 3. [6] Longitudinal section through an ovule of *Ornithogalum*. The funicle or stalk of the ovule is seen to the left, the ovule proper to the right. In the latter there is a large central space, the embryo-sac which contains certain small cells; towards the apex two together of which one is the egg-cell and the other a synergida, at the base two antipodal cells are represented. Around the embryo-sac is a layer of nucellar tissue one cell thick, whilst below, this tissue is more bulky (contents dotted). Around the nucellus are the integuments. A pollen-tube has grown down the micropyle and perforated the apex of the embryo-sac. It is represented in contact with the egg-cell and one synergida. The other synergida is not shown; ×100. (Partly after Strasburger.)

Both categories of pollen-grains are competent to develop tubes and to fertilize the ovules. Under these circumstances it would be very interesting to know what exactly happens when pollen-grains of both these categories are present on one and the same stigma; whether (as is probable) both develop pollen-tubes, whether both

sets of tubes reach the ovary, or whether one set receives a check of some sort. In fact we want to know whether foreign pollen is prepotent over own pollen (where both are competent to fertilize), and if so how the prepotency is accomplished. This and a host of similar problems await solution.

Passing on now to the union of spermatoplasm and ooplasm it is first of all necessary to describe the structure of the ovule in some detail. The egg-cell which has to be fertilized forms but a small portion of the ovule. It is produced in Flowering Plants within a large cell prominently developed and termed the *Embryo-sac*. This embryo-sac is one of the cells of the central portion of the ovule known as the *Nucellus*, and this cell as the time of maturation of the ovule approaches grows much in size, in part at the expense of its neighbours. Ultimately the embryo-sac occupies a large portion of the nucellus, being still inclosed by a layer of small nucellar cells. Outside this are the integuments. They are not completely closed, but at one spot an opening (the *micropyle*) is left, the entrance by which the pollen-tube gains access to the embryo-sac. The general relations of the embryo-sac to the other portions of the ovule are shown in fig. 315[6], a longitudinal section of the ovule of *Ornithogalum*. In fig. 316 three stages of the embryo-sac of *Monotropa* are shown just at the time of fertilization. At an earlier stage the embryo-sac is a uni-nucleate cell, and before the arrival of the pollen-tube at the micropyle its contents divide up into a number of small cells, which, though devoid of cell-membranes, are readily distinguishable from one another. At the apical or micropylar end three of these cells are situated. The two uppermost, side by side, are known as the *synergidæ*, whilst close below them and slightly to one side (*cf.* fig. 316) is the egg-cell, destined to be fertilized. These three cells constitute the "egg-apparatus". At the other extremity of the embryo-sac, *i.e.* at the base, three cells are present which are known as the *antipodal* cells. These, soon after their formation, develop walls around themselves and appear to play no part in subsequent phenomena. Besides these, there are two nuclei (the so-called *polar* nuclei) lying in the protoplasm of the embryo-sac, one close above the antipodals, the other just below the egg-apparatus (fig. 316[1]). These two approach one another at about the moment of fertilization and fuse (figs. 316[2] and 316[3]) about midway between egg-apparatus and antipodals. They give rise ultimately to the food-material which nourishes the young fertilized egg-cell during its early stages of development.

The egg-cell and its attendant synergidæ contain each a well-marked nucleus and vacuoles. In the egg-cell the vacuole is above the nucleus (fig. 316[3]), in the synergidæ the vacuoles are below the nuclei (fig. 316[2]). The nucleus of the egg-cell is often very large. The structure and changes of cell-nuclei have already been briefly reviewed at vol. i. p. 581.

Meanwhile, in the pollen-tube changes have also taken place. Actually in the pollen-cell before the pollen-tube is produced two nuclei are present. Though both of these enter the tube one is quite sterile and soon atrophies. The other, however, surrounded by a small portion of protoplasm, but destitute of wall, constitutes the male sexual cell. It is carried, embedded in the general protoplasm of the pollen-

tube, near the tip, and so is gradually brought down to the embryo-sac. The male cell divides into two, and both are brought down to the embryo-sac; these two male cells are both of them used in the process of fertilization. When the tip of the pollen-tube reaches the micropyle (as in fig. 315[6], though the contained male cells are not shown), the male sexual cells are well up to the end of the tube. The pollen-tube forces its way down the micropyle, and perforates the apex of the embryo-sac. The tip of the tube is now opened, and the male sexual cells pass out, and, traversing the synergidæ, enter the embryo-sac. The synergidæ seem to promote this transfer of the male sexual cells, though the precise part played by them is not fully understood. With the passage of the male cell the synergidæ collapse and shrivel; their part is played. One of the two male cells enters the egg-cell, and its nucleus approaches and fuses with the nucleus of the egg. The other approaches the polar nuclei (shown in process of fusion in figs. 316[2] and [3]) and with them takes part in an act of triple fusion. The result of this triple fusion is the definitive nucleus of the embryo-sac from which the endosperm is produced. Thus it seems that two several processes of fertilization take place in the embryo-sac. From the one the embryo is produced, from the other (the result of a triple fusion) the food-tissue at the cost of which the embryo develops.

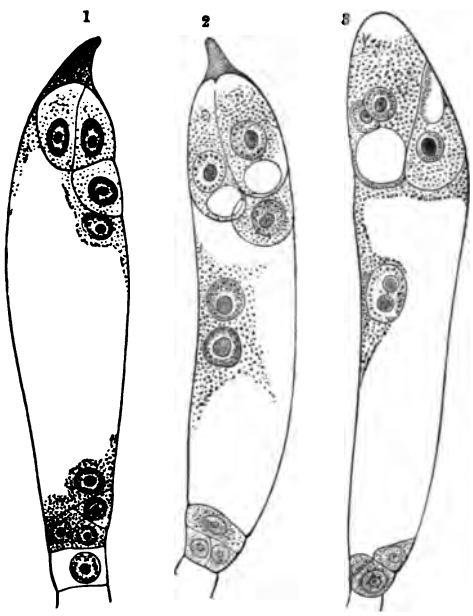

Fig. 316.—Embryo-sac of *Monotropa*.

Three stages are shown just preceding fertilization, in the order [1], [2], [3]. In each of them we see the group of antipodal cells at the base, and the egg-apparatus at the apex. [1] and [2] show the two synergidæ side by side and the egg-cell adjacent to them. In [3] the synergidæ are on the left, seen through one another, both their nuclei showing; the egg-cell on the right. The process of fusion of the so-called polar nuclei is shown in the figs.; in [1] they are not yet detached from their respective groups, in [2] they have approached one another, in [3] they are in process of fusion.

The fertilized egg-cell, which we may now term the *embryonic cell*, soon gives indication of the change which it has undergone. It secretes a cell-wall around itself. Had it not been fertilized the egg-cell would have remained naked and inactive, and ultimately would have perished.

In the account of the fertilization of the Angiosperm just given, the main facts have been related in their barest outline; the discovery of the triple fusion is still quite recent, but its existence has been confirmed in a sufficient number of families of both Monocotyledons and Dicotyledons to arouse the confident expectation that it will prove to occur generally throughout the whole series of Angiospermous plants. The significance of the process is hardly appreciated as yet at its true value, and it will be necessary to wait some years before we see it in its true light. Investigation into the minutest features and processes of ovular morphology and

physiology is now so active that many matters once regarded as settled have come to the front again as open questions.

In the *Gymnosperms*, the group of Flowering Plants with exposed ovules, though the essential facts of fertilization—the fusion of the male sexual cell with the female sexual cell (egg)—are the same as in the *Angiosperms*, just described, in many subordinate points they exhibit marked differences. The male flowers of Gymnosperms produce stamens with anthers in which pollen-grains are developed much as in Angiosperms. The arrangements, however, associated with the production of ovules are simpler than in the Angiosperms, and recall to some extent the characters presented by certain Ferns. In the Ferns and other Cryptogams it will be remembered that fertilization is under water, whilst in Phanerogams this is accomplished through the medium of the air (*cf.* p. 71). The spermatozoids of the Cryptogams reach the egg-cell in the oogonium or archegonium by swimming; they are naked protoplasmic masses, and need no enveloping and protective cell-wall. It is otherwise in the Phanerogams, where aërial fertilization obtains. Here a membrane around the spermatoplasm is of great value; it serves to protect the contents of the pollen-grain during its journey through the air, and afterwards, in connection with the pollen-tube, is of the utmost value in conveying the male sexual cell to the egg. It is interesting to note, however, that in certain Fern-like Gymnosperms, *i.e.* in Cycads, and in *Ginkgo*, although pollen-tubes are produced, they do not reach to the egg-cell, but liberate motile spermatozoids which swim the last bit of the way. Cryptogamic methods are thus retained in the most primitive Gymnosperms.

The ovules of Gymnosperms show the grosser characters of those of Angiosperms. In fig. 335[7] is shown a scale from a female flower (cone) of the Scotch Pine (*Pinus sylvestris*). Right and left at its base are the ovules, two in number. Each ovule exhibits a central nucellus and a conspicuous integument surrounding it, leaving a wide, funnel-shaped micropyle giving access to the tip of the nucellus (*cf.* also fig. 208[8], p. 74, representing an ovule of *Cycas*). Within the nucellus a large cell becomes marked out, as in Angiosperms; this is the embryo-sac. The embryo-sac becomes filled with an extensive tissue, the endosperm, and produces at its apical end (towards the micropyle) a number of egg-cells. These vary in number from 2–15 in various Gymnosperms, but in any case they are all assembled together beneath the micropyle. Associated with each egg-cell is a neck, recalling that structure in the archegonium (or amphigonium) of Ferns (*cf.* p. 67). Fig. 315[2] shows the tip of a gymnospermic ovule in section, considerably enlarged. Note the funnel-shaped micropyle (with germinating pollen-grains in it) and two large, oval egg-cells in the endosperm below. The slight shading above the tips of the two egg-cells indicates the necks. The contents of the egg-cells in this figure have already given rise to several cells, as in the stage represented fertilization has just occurred. The cells here shown in *Ephedra* (fig. 315[2]), or in most other Gymnosperms a limited number of cells (often four) cut off at the base of each egg-cell, develop into little embryos, of which, however, ultimately one only survives for each

seed. A characteristic feature, occurring shortly before fertilization, is the cutting-off of a small cell from the summit of the egg-cell. This little bi-convex cell (shown at the tip of the right-hand egg in fig. 315 [2]) is known as the "ventral canal-cell". A similar cell is cut off in the Ferns, &c., and lies at the base of the neck of the archegonium just above the egg-cell. It is afterwards absorbed.

From a comparison of the structures in the ovule of a Gymnosperm with those arising on the Fern-prothallium, or Moss-plant, it seems probable that the egg-cell, with its neck in the former, corresponds to the archegonium of the latter, though the archegonium in the Gymnosperm is somewhat reduced when compared with the exposed archegonium of Ferns and Mosses.

The number of egg-cells (=archegonia) produced in the ovule of a Gymnosperm is various. In the Spruce Fir and Pine there are from 3 to 5, in the Cypress and Juniper 5 to 15. In the Firs and Pines the egg-cells are well isolated from one another by layers of endosperm, in which they are embedded; in Cypresses and Junipers the egg-cells are all in immediate contact, forming a rosette-like cluster at the top of the endosperm under the micropyle. The tissue in which they lie embedded, the endosperm, is in Gymnosperms pretty extensive, and being well-stocked with food-materials, forms, after fertilization, a nutritive bed for the young developing embryos, and is ultimately absorbed by them.

In the Angiosperms, on the other hand, the ovules are not exposed on open scales, as in Gymnosperms, but inclosed in definite chambers, the ovaries. Pollen is brought to the stigma (not to the micropyle, as in Gymnosperms), and fertilization is accomplished by the development of pollen-tubes, which penetrate the tissues of the style to the ovules. In Gymnosperms there are no ovaries or styles or stigmas. Pollen is brought by the wind direct to the micropyle of the ovules. Various arrangements exist for bringing the pollen-grains into the micropyle and for holding them there. Just at the time when pollen is liberated from the male flowers the micropyle is opened wide, and its lining cells are rendered sticky by a mucilaginous secretion, so that the pollen brought by the wind sticks to it. This mucilage often projects as a little droplet from the micropyle, and in it the pollen-grains are caught; as this drop gradually dries up and contracts the pollen-grains are sucked into the micropyle, so that the grains come to lie right on the tip of the nucellus of the ovule, from which point they germinate, putting out their tubes (*cf.* fig. 315 [2]). These drops of mucilage can be well seen in early spring on the exposed ovules of the Yew-tree (*Taxus baccata*). This plant is dicecious, and on the female plants the tips of the ovules project from a few scale-like wrappings, which envelop the base of each ovule (*cf.* figs. 336 [2] and 336 [3]). At the time when the male flowers are intrusting their pollen-grains to the wind (usually in March) one may see the female plants, on a sunny morning sparkling in the sunshine as it were with dew-drops. These "dew-drops" are in reality droplets of mucilage, excreted from the micropyles of the ovules, awaiting the chance deposition by the wind of pollen-grains. By and by they dry up and the entangled grains are sucked into the micropyle. In Gymnosperms it is the micropyle, not the stigma, which is pollinated.

After the entrance of the pollen-grains into its mouth the micropyle contracts somewhat, so that the pollen is, so to speak, imprisoned. In Gymnosperms the active development of pollen-tubes only occurs some considerable time after pollination. In the Pine the pollen-grains put out short tubes soon after pollination, but these tubes remain dormant from the spring in which pollination takes place through the summer, autumn, and winter, and only continue their growth after the lapse of about a year. Meanwhile changes take place within the ovule leading to the production of the archegonia with mature egg-cells. Actual fertilization occurs about thirteen months after pollination.

The contents of the pollen-cell, before it leaves the anther (Pines and Firs), or shortly after its reception in the micropyle (*Taxus* and *Cupressus*), divides several times, a number of small cells being cut off at one side of the grain and their substance being separated from the rest of the contents of the grain by cell-membranes. Of these small cells one is the male sexual cell, and ultimately effects fertilization. The big cell (known as the "vegetative cell") produces the pollen-tube. The male sexual cell ("generative cell"), becoming free from its attachments (membranes), passes into the pollen-tube, where it divides into two cells. Ultimately one of these cells fertilizes an egg-cell (the other not being required). In the Juniper, where one pollen-tube fertilizes more than one archegonium, both these generative cells—and possibly others, the result of their further division—would appear to be utilized. The generative cells are carried along with the tube near its growing tip—much as in Angiosperms. Bit by bit the pollen-tube penetrates deeper into the substance of the ovule which forms the floor of the micropyle. Ultimately the tube reaches the neck of an archegonium, and pushes in between the neck-cells, carrying the male cells to the mature egg-cell. In the Cypress and Juniper, where several egg-cells are clustered close together, the tip of the tube widens out, sending a little branch to each of the egg-cells (archegonia), every one of which it is competent to fertilize. In the Pine, Firs, and other Gymnosperms, distinct tubes from separate pollen-grains penetrate to the several archegonia.

Fertilization happens much as in Angiosperms (described on p. 417); the male cell enters the egg-cell, and the male nucleus fuses with the female nucleus. Probably the other elements of the male cell are also taken up by the egg-cell. Indeed, the whole process of pollen-tube development and fertilization is exceedingly similar to these events as described in the Angiosperms. A chief point of difference consists in the absence of distinct cell-walls between the cells which arise in the pollen-grain of the last-named group.

The *development of the embryo from the fertilized egg-cell* is different in Angiosperms and Gymnosperms. In *Angiosperms* the egg-cell, after surrounding itself with a cell-wall, becomes partly attached to the apex of the embryo-sac. It divides by a transverse wall into two cells, one directed towards the micropyle, the other towards the base (chalazal end) of the embryo-sac. The upper (*i.e.* micropylar) of

these two cells stretches, and is repeatedly segmented; thus a string of cells is formed, known as the *suspensor*, bearing at its lower extremity the *embryo-cell*, which gives rise to the greater portion of the young plant. The suspensor, by its elongation, brings the embryo-cell well down into the cavity of the embryo-sac, where it is embedded in the substance of the endosperm which has meanwhile developed. The nutrition of the young plant is thus assured during its early stages. In many Parasites and in Orchids the full-grown embryo shows but little differentiation, and is little more than a mass of cells exhibiting no distinction of stem and leaf-structures; but in the great majority of Angiosperms it soon shows a differentiation into parts—into a little root at one end and a stem at the other, with the rudiments of leaves (*cf.* vol. i. p. 599, figs. 141 [1] and 141 [2]). These leaves, the *cotyledons*, are a conspicuous feature of the embryo, and in several plants they are coloured green by a precocious development of chlorophyll in their tissues (e.g. *Styphnolobium japonicum*). In a large number of plants, as, for instance, the Apple and Oak, Bean and Pea, garden Nasturtium (*Tropæolum*) and Water Chestnut (*Trapa*, *cf.* vol. i. p. 607, figs. 144 [1, 2, 3, 4, 5, 6]), the cotyledons become much enlarged and succulent, and take up large quantities of food-material, which remains stored up in them as reserve-material for the further development of the young plant at germination. When this happens the cotyledons usually come to fill the whole cavity of the seed right up to the integument (*testa*). In the majority of plants, however, the cotyledons remain small and thin, and do not take up the whole reserve of food-material which envelops the embryo. Under these circumstances the embryo is provided with a special reserve-tissue, destined for its consumption when it is separated from the mother-plant. This tissue is analogous to the yolk of a bird's egg, and consists of a tissue of cells filled with fat, starch- and proteid-granules. This food-tissue is variously known as *endosperm*, *albumen*, &c., but the terminology associated with it does not reflect great credit upon the Botanists who are responsible for the introduction of the various terms.

The starting-point for this *reserve-tissue* consists of the nucleus which arises in the embryo-sac from the triple fusion of the two polar nuclei and the second male nucleus already described at p. 417. Around these nuclei a certain amount of protoplasm collects, and after their fusion into the so-called *definitive nucleus* (fig. 316 [3]), a very active cell-division sets in, which results in the formation of a parenchymatous tissue which occupies the embryo-sac and becomes filled with food-materials (fat, starch, and proteids). This tissue is the already-mentioned *reserve-tissue* of the seed or *endosperm*. Most frequently, as we have stated, the embryo enters on a resting period embedded in or adjacent to this reserve, and absorbs it at germination. In other cases, as in the Bean, Oak, &c., as mentioned, the cotyledons of the embryo forthwith take up all this food, so that when the resting-stage comes on, the greatly swollen embryo fills the whole cavity of the seed. This former class of seed is spoken of as *albuminous*, the latter as *ex-albuminous*. There is just this difference between albuminous and ex-albuminous seeds: in the former the embryo only takes up the food-material at germination, in the latter, relatively

early, before the seed enters on its resting-stage. The ultimate fate of the food-material is the same in both cases, *i.e.* to nourish the young plant.

The relations of the *embryo* to its *reserve-tissue* are very various. In many plants, *e.g.* Pimpernel, Wood Sorrel, Snapdragon, and Strawberry-tree (*Anagallis, Oxalis Acetosella, Antirrhinum majus, Arbutus Unedo, cf.* figs. 317 [3, 4, 5, 6, 7, 8, 9, 10]), the straight embryo lies embedded in its reserve-tissue. The same relations obtain in the Rue (*Ruta graveolens, cf.* figs. 317 [1] and 317 [2]), the embryo here being slightly bent; whilst in *Phytolacca decandra* (fig. 317 [11]), on the other hand, the embryo is outside its reserve-tissue, and curved around it like a horse-shoe. In Sapindaceæ and Chenopodiaceæ the embryo is spirally twisted. In the Grasses it is laterally placed to its reserve-tissue (*cf.* vol. i. p. 599, figs. 141 [3] and 141 [4]), and the manner in which it utilizes its reserve has been already fully described in vol. i. p. 604.

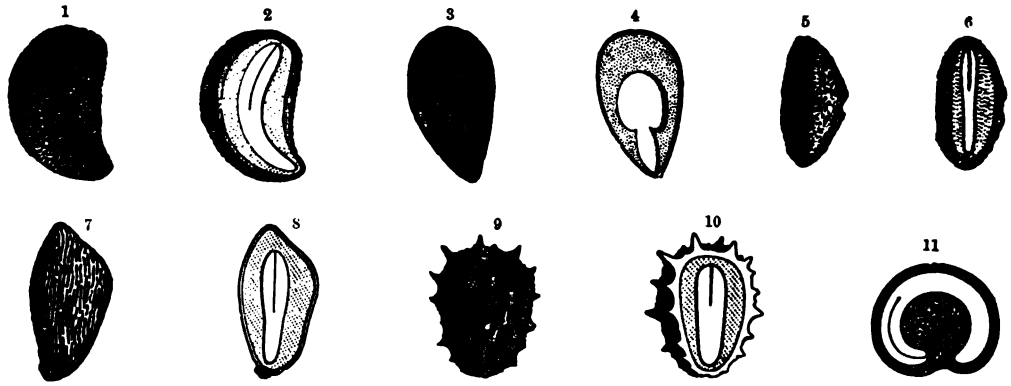

Fig. 317.—Seeds with a Reserve-tissue.

[1] *Ruta graveolens*, the intact seed. [2] Longitudinal section of the same. [3] *Oxalis Acetosella*, intact seed. [4] Longitudinal section of the same. [5] *Anagallis phœnicea*, intact seed. [6] Longitudinal section of the same. [7] *Arbutus Unedo*, intact seed. [8] Longitudinal section of the same. [9] *Antirrhinum majus*, intact seed. [10] Longitudinal section of the same. [11] Longitudinal section of seed of *Phytolacca decandra*. (After Baillon.)

Both the embryo and its reserve-tissue increase at the expense of the tissue immediately external to the embryo-sac; and in the ripe seed very slight traces of this tissue are to be found. Only in relatively few seeds is food stored in this peripheral tissue (*i.e.* in the tissue of the nucellus between the integument and embryo-sac). Under these circumstances this nucellar tissue assumes very much the character of the more usual reserve-tissue (endosperm) which is formed *within* the embryo-sac. Its cells become filled with fat, starch, and proteids, which serve later on as food-material for the young plant. Reserve-tissue when stored *within* the embryo-sac is termed *endosperm*; this, which arises external to the embryo-sac is, in contradistinction, termed *perisperm*.

It is worthy of note that a formation of reserve-tissue does not take place in ovules which are not fertilized. The act of fertilization obviously exerts an influence not limited to the embryo. One may compare this influence to the impulse generated when a stone is thrown into still water. Just as waves travel in ever-widening circles from the centre of disturbance, so it is with the changes in the ovule: first, changes are noticeable in the egg-cell, then successively in the embryo-sac,

integuments, in the carpels, and, finally, in the flowering axis which bears the whole of the structures concerned. These changes, which become manifest in the form of growth, are executed on a definite plan in every plant, and depend on the peculiar constitution of the protoplasm. The aim of these growth-changes is not difficult to determine. The new organism which has arisen from fertilization must be adequately provided for the future; it is detached sooner or later from its parent-

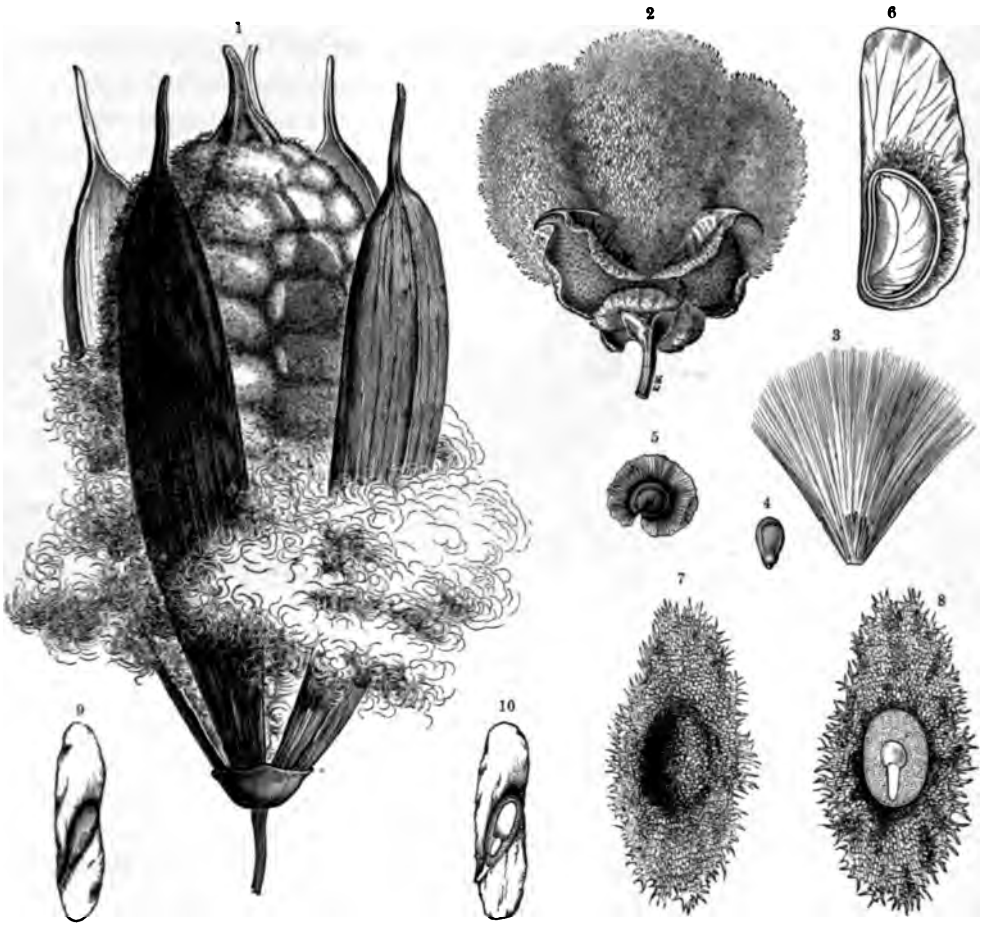

Fig. 318.—Seeds with winged and hairy appendages.

[1] Dehiscent fruit of *Eriodendron*; the seeds embedded in a hairy investment are visible between the valves. [2] Dehiscent fruit of *Gossypium herbaceum*; the mass of seeds is contained in a hairy investment protruding from the valves. [3] Seed of Aspen (*Populus tremula*) with silky appendage. [4] The same seed stripped of its silk. [5] Winged seed of *Lepigonum marginatum*. [6] Longitudinal section of the winged seed of *Vochysia*. [7] Winged seed of *Cinchona*. [8] Longitudinal section of this seed. [9] Winged seed of *Cedrela Toona*. [10] Longitudinal section of same. [4–8] magnified. (Partly after Baillon.)

plant, and has to establish itself in a new place. The embryo requires special equipment for its journey and for its start in life; it requires a means of dispersal and protection against attacks from animals so long as it remains attached to the parent-plant, it requires also protection against unfavourable climatic conditions. These various equipments are provided by peculiar changes in the integument, carpels, and receptacle, changes which are initiated at fertilization.

The integuments of the ovule are altered into the *seed-coat*, which often exhibits a differentiation into two layers. The inner layer takes the form of a delicate, colourless membrane which is rarely hardened, or of a mucilaginous, readily-swelling layer. The outer seed-coat or *testa* shows, however, a great variety of form. It usually consists of several layers of cells, the successive layers of which are frequently very differently fashioned. Sometimes they are soft and membraneous, sometimes rigid and parchment-like, woody or horny, whilst in other cases they may be succulent and fleshy, or converted into a mucilaginous, sticky envelope. The outmost layer of the testa is usually brown, gray, and black, more rarely yellow, white, or red in colour. The significance of the various slimy layers, which on moistening become sticky, of the little pits and furrows, warts, spines, and the like in promoting the firm anchoring of the seed on its germinating bed has already been fully pointed

Fig. 319.—*Salix polaris* with opened fruits showing masses of hairy seeds escaping.

out (*cf.* vol. i. pp. 614–620). Many seeds, in order that they may be distributed by the wind, develop from the outmost layer of the testa wing-like appendages, as, for instance, in the seeds of the Caryophyllaceous *Lepigonum marginatum* (see fig. 318 [5]), in those of the Cinchona-tree (*Cinchona*, figs. 318 [7] and 318 [8]), in the tropical *Vochysia* (fig. 318 [6]) and *Cedrela* (figs. 318 [9] and 318 [10]), and many others. This just-mentioned *Vochysia*-seed is also characterized by the curious wrapping of the cotyledons upon one another (fig. 318 [6]). Often, again, for the same purpose, the superficial cells of the testa grow out, forming a plume or plexus of silky or cottony hairs, as in the Indian species of Cotton-plant (*Gossypium herbaceum*, fig. 318 [2]), and in the cotton-producing *Eriodendron* (fig. 318 [1]). In the seeds of the Oleander (*Nerium Oleander*) the hairs at the apex are longer than those at the base, whilst in the Willow-herb (*Epilobium*) a delicate tuft of long silky hairs is developed at the apex only.

In a considerable number of plants there is developed from the base of the seed, or from its funicle, a curious and special structure, which by the time the seed is ripe envelops the seed like a mantle. This structure is known as the *Aril*. These arils

show very various characters, just as the testa itself may do. In the Willow (*Salix*, fig. 319) and Poplar (*Populus*, figs. 318[3] and 318[4]) it consists of long, delicate silky hairs; in many Passifloraceæ, Sapindaceæ, and Celastrineæ—amongst others, in the well-known Spindle-tree (*Euonymus*), it forms a fleshy, succulent investment, often coloured bright red or orange, whilst in the Myristicaceæ it forms a curious, laciniated sheath. In the Nutmeg (*Myristica moschata*) the seed proper constitutes the nutmeg of commerce, whilst the mace is the aril which grows around this seed. When these accessory structures of the seed are only developed locally as little ridges or bumps at the base of the seed, or on the funicle, they are known as *caruncles*. A well-marked, fleshy cock's-comb-like caruncle is formed on the seeds of the Celandine (*Chelidonium majus*). When the swelling is limited to the point of attachment of the seed to its funicle, one speaks of a *hilar caruncle*, as is seen in the Pansy (*cf.* figs. 320[1] and 320[2]). The spot where the seed is attached to its stalk is known as the *hilum*, and is readily seen, even when distinguished by no special swelling or caruncle, on a detached seed. It is usually a well-defined area, coloured differently from the rest of the testa, sometimes projecting, sometimes slightly excavated, and not infrequently having the form of a well-marked groove (see fig. 320[5]). At the place where separation has occurred there is a kind of scar, the *hilar scar* (sometimes called the *omphalodium*). The spot occupied by the micropyle is often recognizable on the ripe seed, and may be termed the *micropylar scar*. It usually appears as a little hole or pin-point depression bordered by peculiar tissue. In curved (campylotropous) seeds, the micropylar and hilar scars are seen near together, but not so close as to be inseparable (figs. 320[6] and 320[7]; in 320[6] the point indicates the position of the micropylar, the excavation that of the hilar scar). In the Castor-oil plant (*Ricinus communis*, figs. 320[3] and 320[4]), the lips of the micropyle undergo considerable growth, forming a little cushion or micropylar caruncle, very conspicuous at the top of the seed.

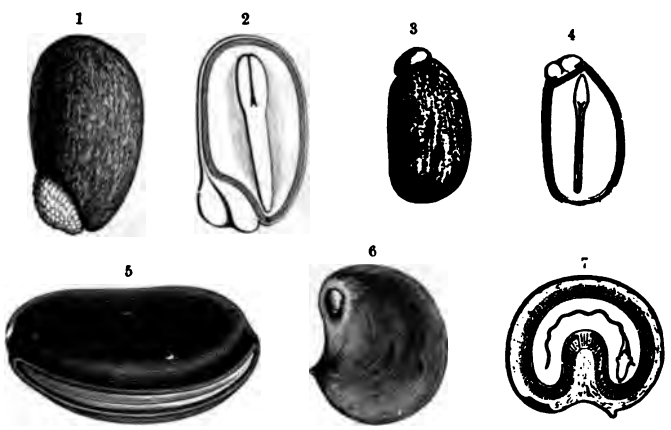

Fig. 320.—Seeds with caruncles and hilar scars.

[1] Seed of *Viola tricolor*. [2] The same in longitudinal section. [3] Seed of *Ricinus communis*. [4] The same in longitudinal section. [5] Seed of *Physostigma venenosum*. [6] Seed of *Anamirta Cocculus*. [7] The same in longitudinal section. (After Baillon.)

Corresponding to the externally visible hilar and micropylar scars is a curious internal structure of this portion of the seed-coat. This will be more intelligible when it is explained that in many cases the water needed by the resting embryo for its further development can only be absorbed at these spots. The tissue here,

indeed, serves as a mechanism for supplying the embryo with moisture from the germinating bed. For its successful operation it is necessary that the seed should be favourably situated upon the soil, in other words, that these portions of tissue which conduct water to the embryo should be in contact with the damp earth. Such a position is promoted by the fact that in cases of the kind under discussion the seed is so formed and its centre of gravity so adjusted that in falling the hilar scar generally comes to lie underneath. The tissue here is more or less porous and provided with lacunæ, so that water can be taken up and transmitted to the embryo. Not infrequently it consists of loose stellate cells, and water is absorbed from the environment as by a sponge and placed at the service of the deeper-lying regions of the seed, especially the embryo.

Fig. 321.—[1] Branch of Mezereon (*Daphne Mezereum*) with berries. [2] Fruiting branch of the Lime (*Tilia*) with downy hairs investing the nut-like fruits. [3] Longitudinal section through a fruit of the Lime. [1] and [2] natural size. [3] magnified.

In those seeds, on the other hand, in which water is not absorbed at definite spots but over the whole surface, there exist scattered over the surface between the thickened impervious cells, which form the greater portion of the investment, special strings of cells or minute canals which at the proper time are permeable and serve for the taking up of water. Thus, for instance, in the hard, round, black seeds of the Indian Shot (*Canna*), the testa, consisting as it does of an outer layer of thick-walled palisade-cells with several layers of transversely-stretched stony cells beneath, constitutes an exceedingly strong protection for the embryo. But over the whole surface of the seed are distributed tiny depressions, at the base of each of which a stomate opens. Each of these stomates leads into a canal of minute proportions traversing the layers of the testa and adequate for taking up water at germination.

Intimately connected with the developing seeds is the structure in which they are contained, and in which they were originally fertilized. This is known at the time of fertilization as the *pistil* or *ovary*, and later, when the seeds are ripe, as the

pericarp, seed-capsule, or *case.* As a rule this structure is known to Botanists as the *fruit,* though this designation is open to criticism. In the broad sense the fruit in Phanerogams should include everything which undergoes alteration after fertilization either in the flower or flowering axis. All these changes take place in the parts in question for the purpose of promoting the interests of the embryo, and properly equipping it when the time comes for its severance from the parent plant, consequently the whole of the structures which participate in this object should be regarded as the fruit. From this point of view the seed-case or pericarp (derived from the pistil) constitutes only a portion of the fruit. Since, however, the seed-

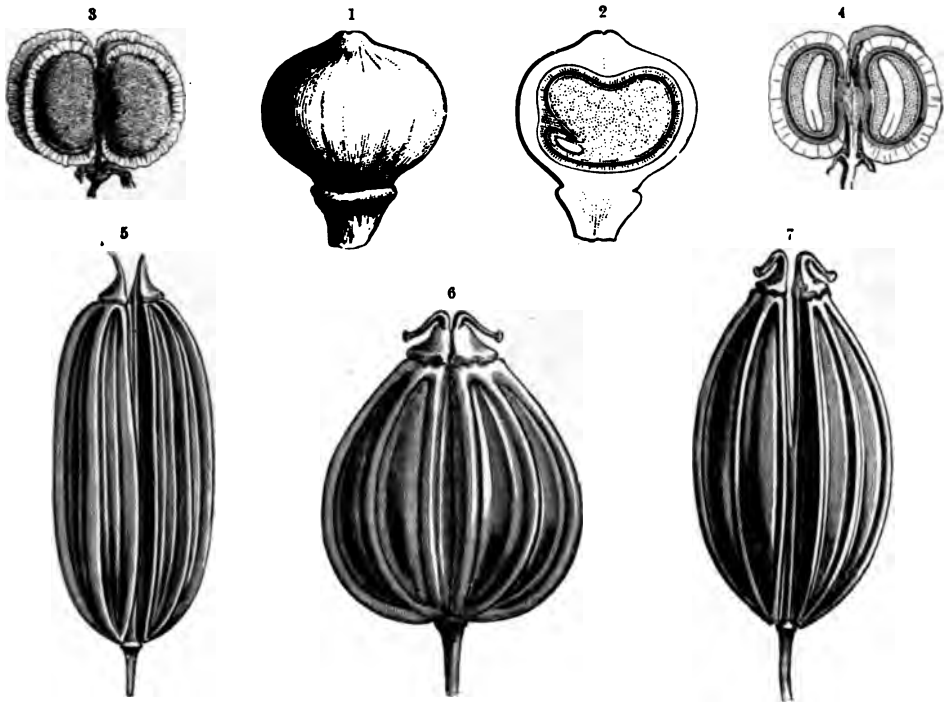

Fig. 322.—Indehiscent fruits and schizocarps.

[1] Drupaceous Nut of *Fumaria.* [2] The same in longitudinal section. [3] Indehiscent fruit of *Callitriche.* [4] The same in longitudinal section. [5] Schizocarp of *Fœniculum aromaticum.* [6] Schizocarp of *Petroselinum sativum.* [7] Schizocarp of *Carum carvi.* All the figs. enlarged. (After Baillon.)

case in a very large number of cases approximates to and essentially constitutes the whole fruit, we will not press our quarrel with the descriptive botanists to the point of pedantry, but having made our protest fall into line with the usual terminology.

Types of Fruit.—When the seed-case derived from the pistil becomes altogether fleshy and succulent, the fruit is termed a *Berry.* From inferior pistils arise inferior berries. From superior pistils superior berries. The berries of the Bitter-sweet (*Solanum Dulcamara*), of the Deadly Nightshade (*Atropa Belladonna*), of the Barberry (*Berberis vulgaris*), and of the Vine (*Vitis vinifera*) are superior; those of the Mistletoe (*Viscum album*), and of the Gooseberry (*Ribes Grossularia*) are inferior. The berry of the Mezereon (*Daphne Mezereum*) is also superior, but is

peculiar in that the flesh is contributed not only by the pericarp proper (fruit-wall), but also by the outmost layer of the seed-coat. It is the inner layer of the seed-coat which here gives rise to the stone.

When the outer part of the pericarp is fleshy, and the inner part which immediately invests the seeds stony, the fruit is called a *Drupe* or stone-fruit. The

Fig. 323.—Winged Fruits.

[1] Cluster of fruits of the Ash (*Fraxinus excelsior*). [2] A single fruit artificially opened. [3] Seed of *Fraxinus excelsior*. [4] The same seed in longitudinal section. [5] Fruit of *Banisteria*. [6] Fruit of *Angelica sylvestris*. [7] Fruit of *Ailanthus glandulosa*, the central, seed-containing portion seen in section. (Partly after Baillon.)

majority of drupes, *e.g.* the Sloe (*Prunus spinosa*), and Cherry (*Prunus avium*), contain only a single stone and seed. That of the Buckthorn (*Rhamnus*) contains two stones, each of which contains a seed, whilst that of the Elder (*Sambucus nigra*), usually described as a berry, is in reality a drupe containing from 2–4 stones each with one seed.

In a very large number of fruits the pericarp is entirely dry. These *dry* fruits

may be distinguished into *Indehiscent fruits, Schizocarps,* and dry *Dehiscent fruits.* The indehiscent fruit never opens spontaneously. When ripe it comes away with the inclosed seed and is concerned in the dispersal and establishment of this seed. The indehiscent fruit is termed a *Nut* when it arises from a pistil constituted of more than one carpel, as in the Lime (*Tilia,* figs. 321 [2] and 321 [3]), an *Achene* when produced from a monocarpellary pistil. When the contained seed is entirely fused with the lining of the fruit-wall, as in Grasses (*cf.* vol. i. p. 599, fig. 141 [3]), the fruit

Fig. 324.—Flowering branch of *Banksia serrata* with thick-walled dehiscent capsules. (After Baillon.)

is termed a *Caryopsis.* Sometimes the wall of the nut consists of an outer more fleshy layer, and an inner harder layer after the manner of a drupe. Such a fruit, as in the Fumitory (*Fumaria,* figs. 322 [1] and 322 [2]), is known as a drupaceous nut. As a rule the nut is uni-loculate and contains but a single seed; and this notwithstanding the terms of our definition, according to which a nut is the product of a multi-carpellary ovary. Actually in development all the chambers but one (which contains the ripe seed) atrophy. Only rarely are nuts multilocular, as in the Water-star (*Callitriche,* figs. 322 [3] and 322 [4]) which has a 4-chambered nut and forms a transition to the schizocarp.

The *Schizocarp* may be regarded as consisting of a number of Achenes united together. Two or more carpels, each containing a seed, remain joined together during

ripening, and only later, when the seed is ripe, do they separate from one another, as though the original fruit had been cut into its component parts by a sharp knife. Each of these components (known as *Mericarps*) remains indehiscent like an achene, and is distributed with its contained seed. As a type of these schizocarps the Mallow (*Malva*) may be taken. In the Umbelliferæ the two mericarps into which the schizocarp splits remain for a long time suspended from the tips of a forked prolongation of the axis, as in the fruits of the Caroway (*Carum carvi*, fig. 322 [7]), Parsley (*Petroselinum*, fig. 322 [6]), and Fennel (*Fœniculum*, fig. 322 [5]).

As already mentioned, the pericarp of many indehiscent fruits assists in the dispersal and establishment of the inclosed seeds. This may happen in two ways. The surface of the fruit may bear hairs, curved bristles, or hooked spines which become attached to the coats of animals; or wings, plumes, &c. may be produced, allowing the fruit to be readily borne away even by the gentlest of breezes. Such winged fruits are termed *Samaras*, and many forms of them are distinguished by the descriptive botanist. To these remarkable fruits, however, we shall return in detail later on when dealing with the dispersal of plants; it will suffice here to indicate briefly a few forms. The fruits of the Ash (*Fraxinus excelsior*) are shown in figs. 323 [1, 2, 3, 4]). The pericarp of each consists actually of two carpels joined together; it is continued into a well-marked membraneous wing. Fig. 323 [7] represents the samara of the Tree of Heaven (*Ailanthus glandulosa*) which is continued below and above the seed-containing portion into a thin, spirally-twisted wing. In the fruit of the Umbelliferous *Angelica sylvestris* (fig. 323 [6]) each half (mericarp) shows a sinuous wing-like fringe on either side, whilst in *Banisteria* (fig. 323 [5]) there projects from the back of each component a membraneous continuation resembling a butterfly's wing.

Dry dehiscent fruits are also known as *Capsules*. When ripe their pericarp, which is quite dry, opens and liberates the seeds in a variety of ways. The empty capsule remains, as a rule, on the parent plant, or comes away in pieces (*valves*) at the time of dehiscence. In neither case, however, has the pericarp any further concern with the seeds after these are once liberated. These capsules are the commonest class of fruit, and as their structure is characteristic of many genera, their various modifications have received distinctive names. When the pericarp arises from a single carpel, and at ripening opens along one side, along the so-called *ventral suture*, whilst the opposite side (the *dorsal suture*) is unsplit, or but partially, one speaks of the fruit as a *Follicle*. As a rule several follicles are collected together in a cluster at the end of the flower-stalk, as, for instance, in Monkshood (*Aconitum*) and in the Star Anise (*Illicium anisatum*, *cf.* fig. 325 [1]); more rarely are they solitary, as in certain species of Larkspur (*Delphinium*). In the Proteaceæ, also, a single follicle arises from each flower, and in the Australian "Wooden Pear" (*Xylomelum pyriforme*, fig. 325 [2]), belonging to this order, the huge and extraordinarily thickened follicle splits completely down the ventral and halfway down the dorsal suture. In *Banksia*, also, of which a head with fruits is shown in fig. 324, the follicles are very hard and woody.

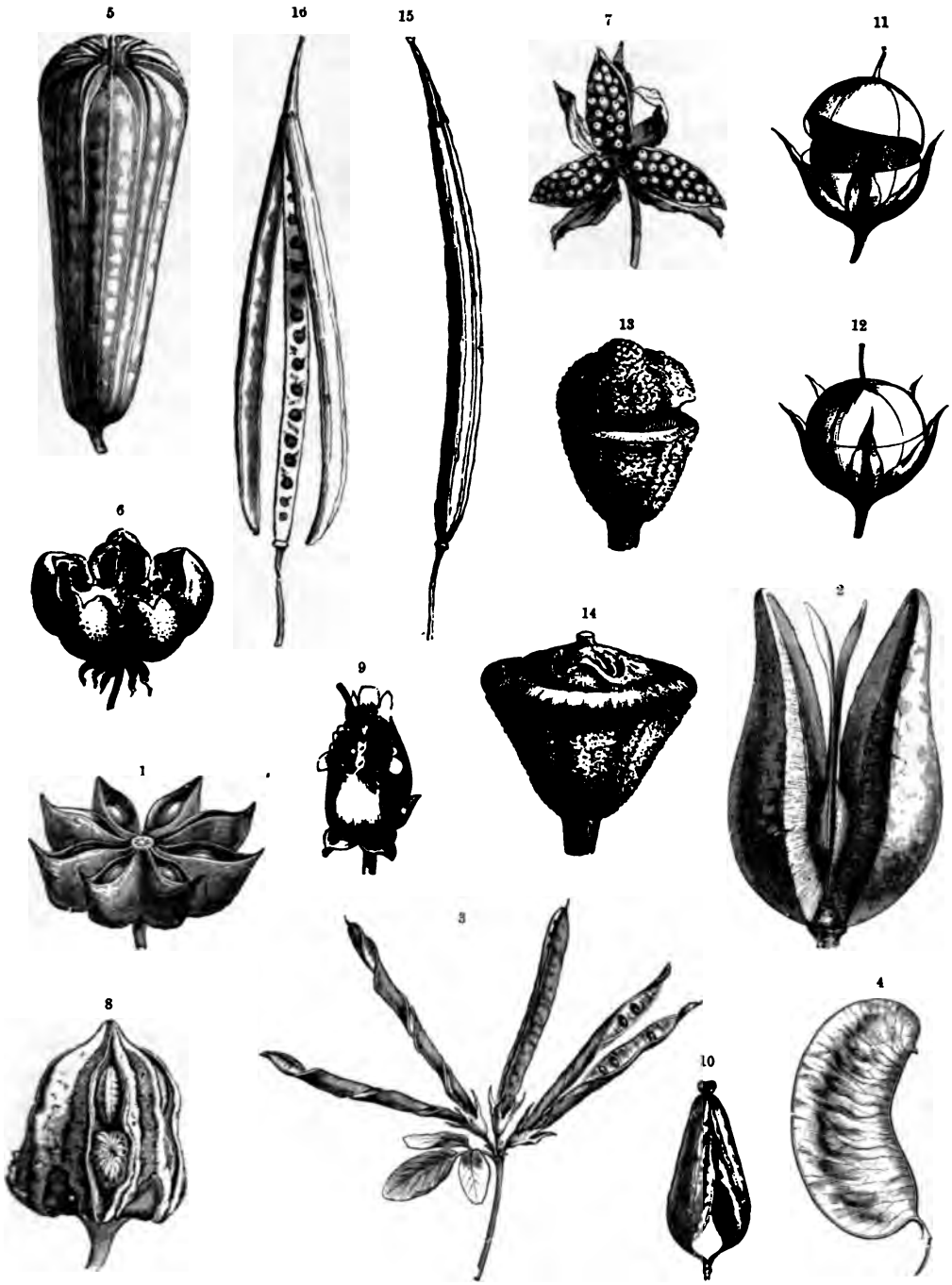

Fig. 325.—Various Capsular Fruits.

[2] Follicles of *Illicium anisatum*. [3] Follicle of *Xylomelum pyriforme*. [5] Pods of *Lotus corniculatus*. [4] Pod of *Cassia angustifolia*. [5] Capsule of *Aristolochia*. [6] Capsule of *Ruta*. [7] Capsule of *Viola*. [8] Capsule of *Oxalis*. [9] Capsule of *Antirrhinum*. [10] Capsule of *Cinchona*. [11, 12] Capsules of *Anagallis*. [13, 14] Capsules of *Eucalyptus*. [15, 16] Siliquas of *Brassica*. [2, 10, 11] enlarged; the rest natural size. (After Baillon.)

Like the follicle, the *Legume* or *Pod* arises from a single carpel, but on ripening it splits down *both* sutures completely to the base into two valves, which at the moment of dehiscence become rolled up spirally. This type of fruit is extremely common in the Leguminosæ. As examples may be mentioned *Lotus corniculatus* (fig. 325 [3]) and the Senna (*Cassia angustifolia*, fig. 325 [4]).

Dry dehiscent fruits, the product of two or more carpels, are termed *capsules* in the restricted sense. We may distinguish several types of capsules; (1) such as split into valves from the apex, as in the Birthwort (*Aristolochia*, fig. 325 [5]), Rue (*Ruta*, fig. 325 [6]) and Violet (*Viola*, fig. 325 [7]); (2) such as open by means of teeth restricted to the apex, as in Caryophyllaceæ; (3) such as split longitudinally down the side-walls, the actual cavities of the fruit opening, as in the Wood Sorrel (*Oxalis*, fig. 325 [8]); (4) such as produce several large apertures by the folding back of teeth, as in the Snapdragon (*Antirrhinum*, fig. 325 [9]); and (5) such as form numerous

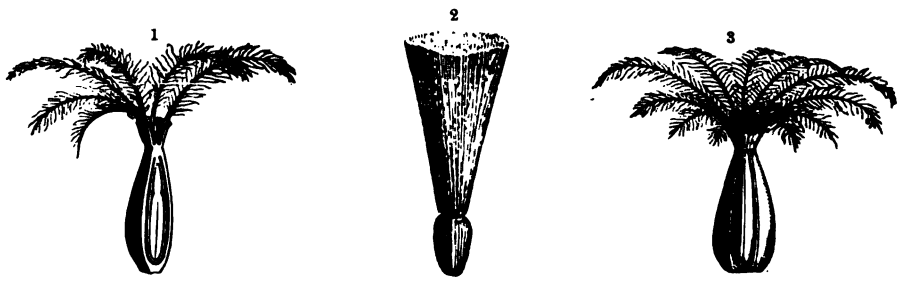

Fig. 326.—Achenes provided with a plume or pappus.

[1] Fruit of Valerian (*Valeriana officinalis*). [2] The same in longitudinal section. [3] Fruit of the Artichoke (*Cynara Scolymus*). (After Baillon.)

small pores by the shrivelling of restricted areas, as in the Poppy (*Papaver*). The capsules of the Cinchona-tree (*Cinchona*, fig. 325 [10]) split into two valves, which remain attached at the apex, separating at the base only; whilst many capsules dehisce transversely, a lid being removed, as in the Pimpernel (*Anagallis*, figs. 325 [11] and 325 [12]) and *Eucalyptus* (figs. 325 [13] and 325 [14]).

A special form of capsule, known as the *Siliqua*, is characteristic of most Crucifers. It is usually described as consisting of two carpels, the exposed walls of which come away, leaving a framework (the *replum*) to which the seeds are attached. Stretched upon this framework is the membrane which formed the ("false") partition of the ovary. This class of fruit is well shown in Honesty (*Lunaria*) and in the Cabbage (*Brassica oleracea*, figs. 325 [15] and 325 [16]). According to the terminology given at p. 75 (4), the two valves which come away correspond to the two outer non-ovule-bearing carpels, whilst the ribs which remain are the two inner ovuliferous carpels.

Though, in a great number of Angiosperms, the various floral-leaves disarticulate and fall away after pollination and fertilization, this is not universally the case; in a considerable number some of them remain behind, undergo various changes, and form an outside investment or appendage to the fruit which plays an important part in the dispersal or preservation of the seeds. The same is true of the bracts

and bracteoles, the leafy structures which are present in the immediate vicinity of the flowers, though not actually included in them. We may distinguish, perhaps, amongst these accessory structures of the fruit, between such as arise from portions of the perianth on the one hand, and such as are formed from bracts and bracteoles on the other. The enumeration of these structures here, however, must be distinctly limited to a few of the more commonly occurring.

A curious form of fruit obtains in the Mulberry (*Morus*). The female flowers

Fig. 327.—The Hornbeam (*Carpinus Betulus*) in fruit.

in this tree are arranged in little catkin-like clusters. Each flower consists of an ovary inclosed in an inconspicuous four-leaved perianth. From each ovary a tiny nut arises; but the ripe fruit resembles a succulent berry rather than a collection of nuts. This is due to the fact that after fertilization, whilst the ovaries are developing into nuts, their perianths become distended and fleshy, altogether concealing the ovaries. Without a knowledge of the mode of development, the perianth might now be readily mistaken for the true fruit-wall (pericarp), and the nut for the seed In several species of Trefoil (e.g. *Trifolium agrarium, badium, spadiceum*) the papilionaceous corolla is yellow. After fertilization this turns brown, dries up and forms a flying-arrangement for the small fruit within (*cf.* figs. 442 [1, 2, 3, 4, 5]).

It very frequently happens that the *Calyx* is retained as an accessory to the

fruit. In the Winter Cherry (*Physalis Alkekengi*), a solanaceous plant often cultivated in gardens, the calyx, originally small and green, becomes much inflated during ripening and forms a bright red bladder inclosing the actual berry; in the Henbane (*Hyoscyamus*), belonging to the same family, the calyx tightly incloses the capsular fruit, its periphery forming a characteristic funnel around the top. In Labiatæ the calyx persists as a short tube, or as a bell or pitcher, at the base of which the actual fruit is found. In the Water Chestnut (*Trapa natans*, *cf.* vol. i. p. 607, fig. 144 [3]) the four segments of the calyx become hardened and persist as four spines arranged cross-wise around the fruit. In many Valerians, Composites, and Scabiouses, the calyx persists, growing, as the fruit ripens, into a radiating crown

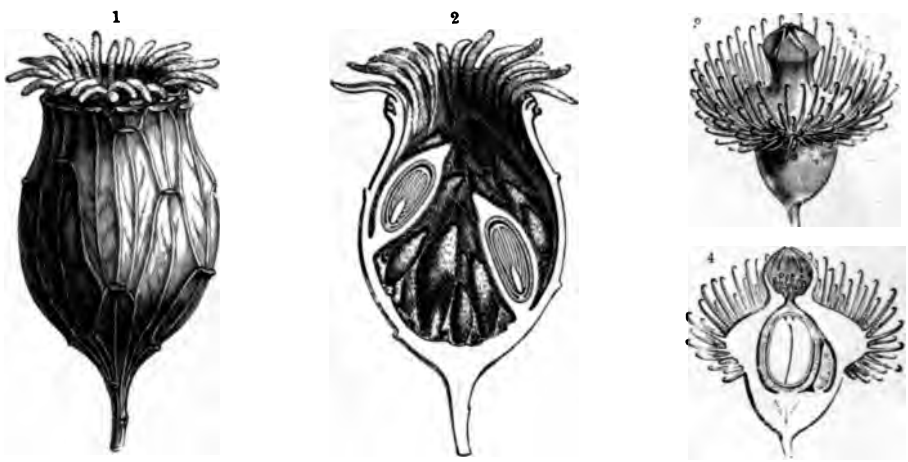

Fig. 328.—Fruits with persistent receptacles.

[1] The Carolina Allspice (*Calycanthus*). [2] Longitudinal section of the same. [3] Fruit of *Agrimonia*. [4] Longitudinal section of the same. (After Baillon.)

of bristles or feathery hairs. This crown, known as a *Pappus*, serves the achene as a parachute (*cf.* figs. 326 [1, 2, 3] and fig. 447).

Amongst the Amentaceæ, trees whose flowers are for the most part destitute of perianth, the *bracts* and *bract-like scales* associated with the flowers often play a prominent part in the fruit. In the Grasses also the same feature is noticeable. In these latter the actual grain is very frequently closely enwrapped by one of the glumes, so tightly indeed, that they easily escape observation, as in Barley, Oats, and many others. The greatest variety of fruit-investment is met with in the Cupuliferæ and allied Amentaceæ, which include the Hornbeam, Hop-hornbeam, Beech, Hazel, and several other well-known trees. The actual fruit in all these is a nut, but inclosed in a peculiar involucre-like sheath (the *cupule*) derived from bract-like scales external to the flowers. In the Oak (*Quercus*) the cupule is cup-like (figs. 329 [1] and 329 [2]); in the Beech (*Fagus*) it completely envelops the paired triangular nuts, and is spiny outside, at ripening it bursts into four valves like a capsule; in the Chestnut (*Castanea*) it is extremely prickly, and, as in the Beech, bursts into valves (fig. 339 [4]); in the Hazel (*Corylus*) it forms a laciniated, leathery envelope to the nuts (fig. 235, p. 147), whilst in the Hornbeam (*Carpinus*, fig. 327)

it has the form of a three-lobed open scale, to the base of which the ribbed nut is attached. Finally, in the Hop-hornbeam (*Ostrya*, fig. 437 [6]) it forms a loose papery envelope.

The *Receptacle* of the flower is not infrequently a conspicuous feature in connection with the fruit. This is well shown in the Carolina Allspice, in Roses, and in Pomaceæ. In the Carolina Allspice (*Calycanthus*, figs. 328 [1] and 328 [2]) an excavated pitcher-like receptacle, invested on the outside with scales, incloses the achenes; in the Rose there is a similar inclosure, here smooth and fleshy, and bearing a five-leaved calyx above, this constitutes the hip. In the Apple, Pear, Quince, and other Pomaceæ, the receptacle forms an extremely succulent mass, in which the actual fruit is imbedded, and with which it is entirely fused (*e.g.* Quince, *Cydonia*, fig. 330 [2]). In the Strawberry (*Fragaria*), on the other hand, the fleshy receptacle is convex, and bears the little achenes scattered over its surface. Not always, however, is the receptacle fleshy; thus, in the Agrimony (*Agrimonia Eupatoria*, figs. 328 [3] and 328 [4]) it forms a dry and woody inclosure for the one or two achenes, and is provided with numerous stiff hooked bristles on its periphery.

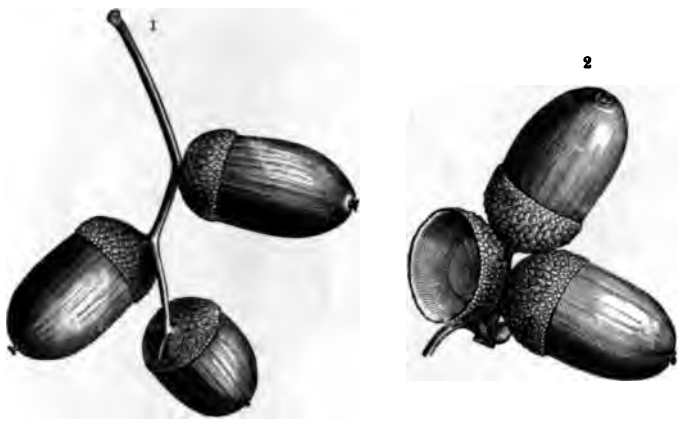

Fig. 329.—Fruits with Cupules

[1] *Quercus pedunculata.* [2] *Quercus sessiliflora.*

Much less frequently does the *flower-stalk* (pedicel) take a share in the fruit formation. This is so, however, in Anacardiaceæ, in some Rhamnaceæ, and in a few other groups. Thus, for instance, in the tree which produces Cashew-nuts (*Anacardium occidentale*, fig. 330 [1]), the upper portion of the pedicel swells up into a fleshy pear-like structure; on its summit is perched the kidney-shaped nut with its inclosed seed. In *Hovenia dulcis* (allied to the Buckthorn) a similar arrangement prevails, the flower-stalks are swollen, and contain a sweet red pulp appreciated by the Chinese and Japanese. To these instances may be added the Fig (*Ficus*, *cf.* figs. 240 [10] and 240 [11], p. 157), in which the whole receptacle of the inflorescence is excavated, urn-wise, and becomes very succulent on ripening. The little grains inside, commonly taken for seeds, are in reality the actual fruits or nuts, each of which contains a seed. As a final instance may be mentioned the polygonaceous *Brunnichia africana* from west tropical Africa; in this case the flower-stalk becomes winged down either side, from its point of insertion up to the nut at its apex. It thus serves as a distributing organ for the fruit.

In many plants whose flowers are clustered very close together it often happens

that the fruits of the several flowers as they increase in size become more or less fused together; or the axis which bears them, or other associated parts, become fleshy forming a succulent matrix for the individual fruits. Such a mass of fruits is termed a *collective fruit*. Good examples of this are the Mulberry (*Morus*), the Pine-apple *Ananassa sativa*), Piperaceæ, *e.g.* Betel Pepper (*Piper Betle*, fig. 331 [1]); and Artocarpeæ, *e.g.* the Bread-fruit (*Artocarpus incisa*, fig. 332) and Jack-fruit (*Artocarpus integrifolia*). With these collective fruits may be contrasted the clustered crowded

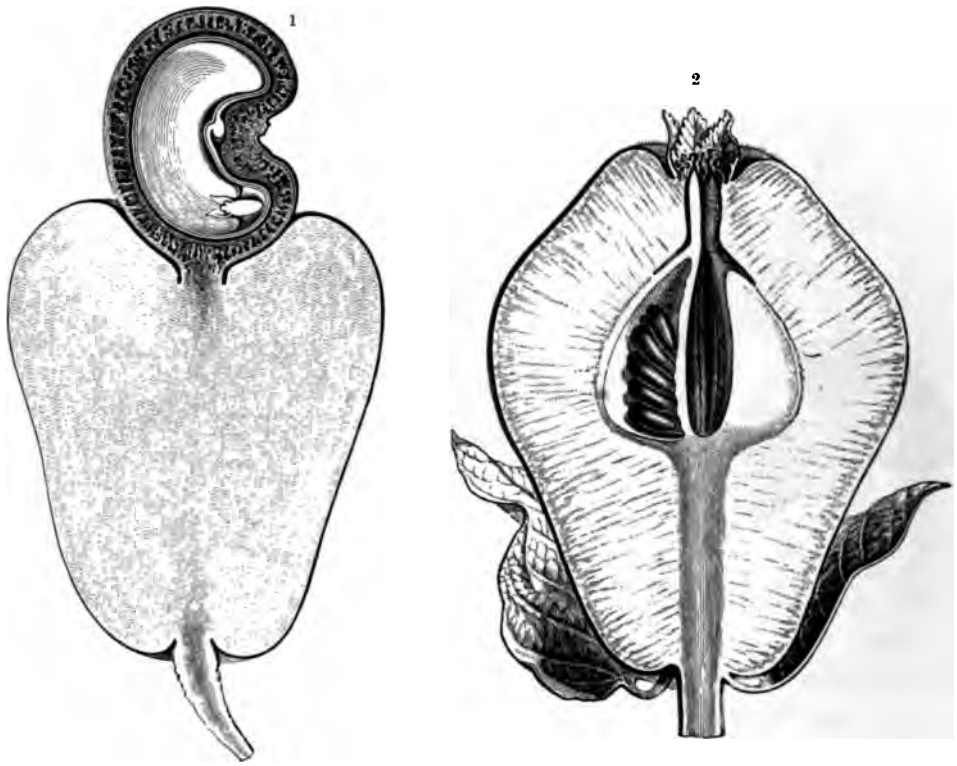

Fig. 330.—Fruits in whose structure the receptacle and pedicel take a share.

[1] Longitudinal section of the fruit of the Cashew-nut Tree (*Anacardium occidentale*). [2] Longitudinal section through a Quince (*Cydonia*). (After Baillon.)

carpels produced from *single flowers* (*aggregate fruits*), such as the Raspberry (*Rubus Idæus*), *Calycanthus*, Rose, &c., already described, also many Anonaceæ, as, for instance, the West-Indian Sour-sop (*Anona muricata*, fig. 331 [4]), the Sweet-sop (*Anona squamosa*, figs. 331 [2] and 331 [3]) and Custard-apple (*Anona reticulata*). The terminology that has grown up around the types of fruit described in this paragraph is extremely confusing and slovenly. We propose to call the compound fruit arising from a number of crowded flowers a *collective fruit*, that from the carpels of a single flower an *aggregate fruit*. An altogether peculiar fruit is that of the Lotus Lily (*Nelumbium speciosum*, *cf.* figs. 333 and 334). Here the receptacle is enlarged into a huge top-shaped structure in the middle of the flower (fig. 334 [1]); the upper surface of this top is like a honey-comb, and in each "cell", a carpel is sunk as in a socket

(fig. 334 [2]). When the fruit is ripe and dry, these carpels form hard, woody achenes which rattle in their loose sockets like teeth in the jawbone of a skull.

Our descriptions of the fruit and its various forms and modifications relate, so far, solely to the Angiosperms. In the *Gymnosperms*, however, several essential differences are to be noted. The account of their methods of fertilization (pp. 418–420) was left at that stage at which the male sexual cell had fused with the egg-cell. The nucleus of the fertilized egg now moves down to the base (away from the

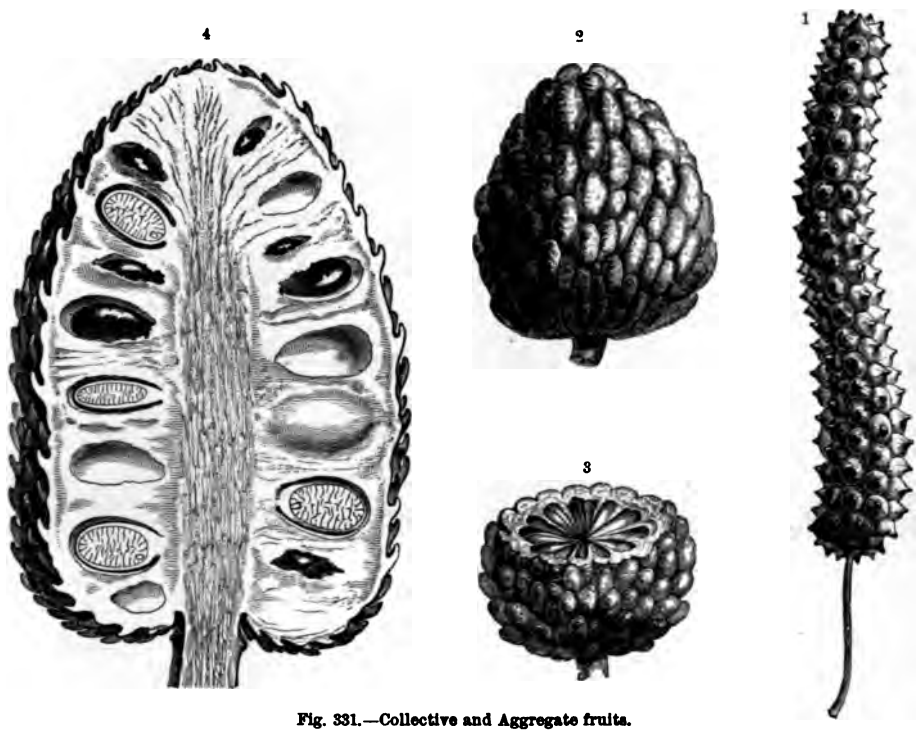

Fig. 331.—Collective and Aggregate fruits.

[1] Collective fruit of Betel Pepper (*Piper Betle*). [2] Aggregate fruit of Sweet-sop (*Anona squamosa*) formed by fusion of the carpels of a single flower. [3] Transverse section of the same. [4] Longitudinal section of the aggregate fruit of the Sour-sop (*Anona muricata*) produced in the same way. (After Baillon.)

micropyle) of the egg-cell and divides several times, each product of its division becoming enveloped in protoplasm and ultimately in a cell-wall. In the Gnetaceæ which many Botanists regard as more nearly allied to the Angiosperms than either of the other two families of Gymnosperms (Coniferæ and Cycadaceæ), there arise in this way from 2–8 daughter-nuclei around each of which protoplasm aggregates, and a cell-membrane is formed (*cf.* fig. 315 [2], p. 415). Between each of these cells there is no connection: each grows out into a tube which penetrates the wall of the egg-cell and pushes its way down into the reserve-food (endosperm) below. From the tip of the tube a small cell, the embryonal cell, is cut off and from this cell by further division and growth an embryo is produced, which is nourished by the food-material. Of the many embryos which are inaugurated, one only comes to maturity, and is found in the ripe seed.

In the Silver Fir, Spruce Fir, Pine, and other Conifers, comprised under the family Abietineæ, the nucleus of the egg-cell divides into four at the base of the egg-cell, and here four little cells are produced, arranged like a rosette at that end. Each of these is divided into three stories, and the four cells forming the middle story elongate, diverge, and grow down into the endosperm, carrying the little embryonal cells at their tips. The four cells of the upper story remain attached to the residue of the egg-cell, and serve as a fulcrum for the elongating tubes—the suspensors. As in the Gnetaceæ, the embryonal cells become modified into embryos,

Fig. 332.—Branch of the Bread-fruit Tree (*Artocarpus incisa*) showing a male inflorescence (sausage-shaped, to the right), a female inflorescence (globular, near the apex) and a collective fruit (to the left). (After Baillon.)

but ultimately only one of them prevails, and, growing at the expense of the food-material, is a conspicuous object in the ripe seed (fig. 335 [6]). A portion of the endosperm remains as a mantle around the embryo, and is only absorbed at germination.

In the Juniper, Arbor Vitæ (*Thuja*), Cypress, and other Conifers belonging to the family Cupressineæ, each egg-cell, after fertilization, gives rise to but a single embryo (though there are exceptions to this rule). Otherwise the events are not very different from those occurring in the Abietineæ.

The *Integument* of the ovule in Gymnosperms forms the seed-envelope (or testa), as in Angiosperms. The *Micropyle* becomes closed up, and the whole testa very hard. In the Pines, Firs, &c. (Abietineæ), the micropyle points *away from* the free margin of the open scale which bears the ovules (fig. 335 [7]), *i.e.* towards the axis of

the cone; in the Cypress and other Cupressineæ, on the other hand, *towards* the free margin of the scale (figs. 337 [3, 4, 6]), and away from the axis of the cone.

In several species, as in the Stone Pine (*Pinus Pinea*) and the Arolla Pine (*Pinus Cembra*), the seed-coat attains a thickness of 1½ to 2 millimetres, so that the seed resembles a nut in appearance. Both these species, indeed, serve as an

Fig. 333.—The Lotus Lily (*Nelumbium speciosum*). (From a photograph.)

article of diet, being eaten like nuts. The seeds of Pines and Fir-trees are provided with a one-sided wing (*cf.* figs. 335 [3, 4, 5]) which plays an important part in their dispersal by wind. In the Maidenhair Tree (*Ginkgo biloba*) the integument of the seed becomes succulent and coloured a bright orange, so that the seed in a way resembles a drupe (*cf.* fig. 337 [7]). In *Cycas revoluta*, also, the integument becomes red and fleshy (*cf.* fig. 208 [7], p. 74).

The ovules of both Abietineæ and Cupressineæ are inserted upon scales of varying form, the insertion of which on the axis of the cone may be broad or narrow (*cf.* figs. 335[7, 8, 9] and 337[3, 4, 6]). These scales form an important constituent of the ripe cone, and are known as the *ovuliferous scales*. In not a few cases, as in the Silver Fir (*Abies pectinata*, figs. 335[1, 2, 3, 4]) and Larch (*Larix*, figs. 335[8] and 337[1]), there exists a second scale, the *bract scale*, beneath each ovuliferous scale, and subtending the same. In the Pine, also, both scales are present, though in the ripe cone there are no signs of the bract-scales at the exterior owing to the fact that they become entirely overgrown and embedded between the big ovuliferous scales.

In the Abietineæ the scales of the cones are inserted in a continuous spiral (*cf.* fig. 335[1], and vol. i. p. 403, fig. 101), whilst in Cupressineæ the scales are inserted in whorls of 2 or 3 scales each (*cf.* figs. 336[6, 7] and 337[3, 5]). In both, the margins of

Fig. 334.—The Lotus Lily (*Nelumbium speciosum*).

[1] Flower from which the perianth-leaves have been removed; expanded receptacle in centre. [2] Longitudinal section through the top-shaped enlargement of the receptacle, showing three carpels embedded in their sockets. (After Baillon.)

the scales overlap, and the seeds are ripened in the slit-like chinks between them (*cf.* 336[6] and 337[5]). The whole assemblage of scales constitutes an aggregate fruit, and is known as a *cone*. The scales may be hard and woody, when we have a woody cone (335[1] and 337[1, 2, 5]); or they may be succulent, giving a fleshy cone. In such fleshy cones very few of the whorls are succulent, the central axis is very short, and the whole structure has much the appearance of a berry, as in the Juniper (*Juniperus communis*, figs. 336[7] and 336[8]).

The section of Gymnosperms known as the Taxineæ do not produce cones. Their seeds arise alone or in pairs at the ends of special short branches, or upon the surface of small fruit-scales. The plum-like seeds of the Maidenhair Tree (*Ginkgo biloba*) are arranged in pairs at the ends of axes which resemble cherry-stalks (see fig. 337[7]). The seeds of the Yew (*Taxus baccata*) occur at the tips of little scale-bearing shoots, and when ripe are almost completely enveloped in a sweet, fleshy, crimson tissue (see figs. 336[1, 4, 5]). This fleshy inclosure, which arises as a circular cushion from the place of insertion of the ovule, is not of the nature of a carpel, it

is an aril. In *Podocarpus*, also, is developed a peculiar structure of the same kind.

In Cycads the seeds are borne upon carpels arranged in cones, and have a woody integument. In some cases they correspond in position to metamorphosed lobes of a carpel (*cf.* fig. 208[7], p. 74), and have the outer layer of their integument developed as a succulent coat. In the Gnetaceæ, the seed at maturity is inclosed

Fig. 335.—Fruit and Seed of Coniferæ.

[1] Cone of the Silver Fir (*Abies pectinata*). [2] Bract scale and ovuliferous scale of the same seen from the outside (the bract scale is pointed). [3] Ovuliferous scale of same seen from above, showing the two winged seeds, and the bract scale behind. [4] Longitudinal section of bract and ovuliferous scales, showing a seed inserted upon the latter. [5] A winged seed of the same. [6] Longitudinal section of the seed. [7] Ovuliferous scale of the Scotch Pine (*Pinus sylvestris*) seen from above; it bears two ovules. [8] Single ovuliferous scale of Larch (*Larix europæa*) showing two ovules on its surface and bract scale (with bristle) below it. [9] Longitudinal section of the ovuliferous scale of the Larch. [1] nat. size; the other figs. enlarged.

in a fleshy "perianth" in *Ephedra*; in *Welwitschia* cone-like collective fruits are produced; finally, in *Gnetum* leaf-structures around the seed unite to form cup-like receptacles for the seeds.

From the brief observations on the manner of fructification of Gymnosperms, it will be seen that their methods are very various, and that, in all cases, they differ from those of Angiosperms. They agree in the common object of producing a

vigorous embryo, and in providing it with adequate safeguards against unfavourable external conditions, and with means of dispersal, when the time comes for the seed to be detached from the parent plant and to take up an independent existence.

Whilst still attached to the parent plant, the embryo needs *protection* against the *ravages* of *animals*, and against *unfavourable climatic conditions*. Means of protection against the former are provided sometimes on the seed-coat, in other cases on the wall of the ovary; or they may be on other structures associated with the flower, or upon the flowering axis itself. These defensive arrangements fall into several groups. First of all, there are thorns, prickles, and spinous bristles, met

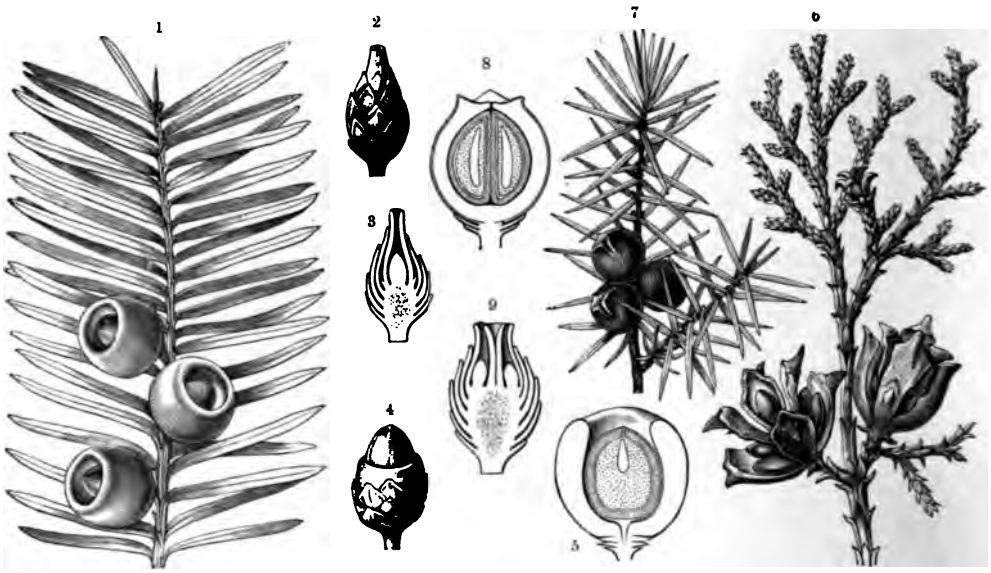

Fig. 336.—Fruits and Seeds of Coniferæ.

[1] Branch of Yew (*Taxus baccata*) with ripe seeds, each inclosed in its aril. [2] Tip of ovule of same projecting from between the scales of the little fertile shoot. [3] Longitudinal section of the same. [4] Young seed of the same only partly inclosed in its aril. [5] Longitudinal section of the ripe seed of the same, showing the aril. [6] Branch of the Arbor Vitæ (*Thuja orientalis*) showing female flowers and ripe, burst cones. [7] Branch of Juniper (*Juniperus communis*) showing berry-like cones. [8] Longitudinal section of one of these cones. [9] Female flower of Juniper. 1, 6, and 7 nat. size; the other figs. enlarged.

with especially on the ovary and immediate envelopes of the fruit. The capsule of the Thorn-apple (*Datura Stramonium*), that of the Anatto (*Bixa Orellana*, see fig. 338), the long 3-valved fruits of *Schrankia* (see fig. 339 [2]), the pods of the Russian Liquorice Plant (*Glycyrrhiza echinata*), the persistent calyx of a steppe-plant, *Arnebia cornuta*, and the cupule of the Chestnut (*Castanea vulgaris*, see fig. 339 [4]) may serve as examples. Several Pines, of which the North American *Pinus serotina* is a type, have cones the scales of which are produced into sharp spines (see fig. 337 [2]), so that the seeds are inaccessible to animals till such time as the scales separate and the winged seeds are committed to the wind. Of interest in this connection are certain Crucifers (*Tetractium quadricorne*, *Matthiola bicornis*, *M. tricuspidata*, fig. 339 [3]) in which, at the end of the fruit just below the scar of the style, 2, 3, or 4 stiff spines are formed, which make these fruits unaccept-

able morsels for animals. A less common condition, and one deserving of special mention, occurs in several Mimosas belonging to the immediate alliance of the Sensitive Plant (e.g. *Mimosa pudica, M. polycarpa, M. hispidula*); of these the last-named may serve as type (see fig. 339[1]). The pods here are densely crowded together, and their dorsal and ventral sutures form a strong framework bearing a double row of short spines. These spines hinder all animals from interfering with

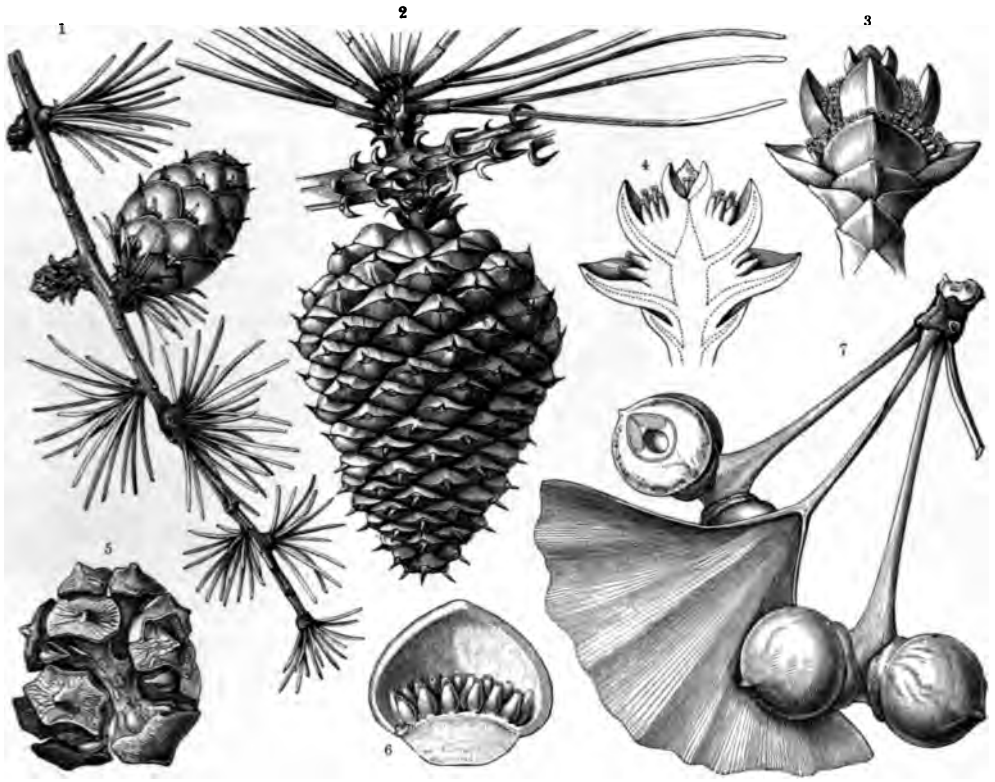

Fig. 337.—Coniferous Fruits and Seeds.

[1] Branch of the Larch (*Larix Europæa*) with ripe cone. [2] Branch of *Pinus serotina* with ripe cone. [3] Female flower of the Cypress. [4] Longitudinal section of the same. [5] Ripe cone of the Cypress (*Cupressus sempervirens*). [6] Single carpel of the Cypress with numerous ovules. [7] Branch of *Ginkgo biloba* with unripe fruit. 1, 2, 5, 7 natural size. The other figures enlarged.

the fruits. As the seeds ripen, the valves fall away from their spiny framework, and are, with their contained seeds, dispersed by the wind. As a rule, the valves break up at this time into one-seeded segments (fig. 339[1]), and being very light in proportion to their area, are carried considerable distances.

In the instances just enumerated the protection is provided only up to the time that the seeds are ripe. With the severance of the seeds from the parent plant the protective function of the spines is at an end. The spinose investment as a rule remains upon the plant, and only rarely, as in the winged fruit of *Centrolobium robustum* (see fig. 339[5]), does the thorny ovary wall (pericarp) become detached with its contained seed. Under these circumstances the spines may play a further

part, either by serving as a mechanism of dispersal, or by fixing the seed in the germinating bed.

In the case of plants with succulent fleshy fruits, the seeds of which are distributed by birds, it would be extremely disadvantageous for the fruits to be provided with spines or prickles when ripe. In point of fact, when such structures are present they often disarticulate and fall away as the fruits ripen, so that birds may have unhindered access to them. The fruits of the leguminous *Mucuna pruriens* are clad during their ripening period with a felt-work of serrated bristles, which contain an irritating fluid. These bristles cause an intolerable itching, or even an eruption of the skin, and, so long as they remain on the fruit, effectively guard it from animals. But as the seeds ripen, and the fruit becomes pulpy, these bristles fall away (so it is stated), and animals are no longer repulsed, but devour the pulp, and so disperse the seeds.

Fig. 338.—Protection of ripening seeds against animals.

The Anatto plant (*Bixa Orellana*) with flowers and fruit. Three of the fruits have opened showing the seeds. (After Baillon.)

The well-known Hips of Roses which ripen in the autumn, do not fall away from the plant, but remain attached. The seeds are contained in hard and tiny nut-like fruits, which are inclosed in the fleshy and excavated receptacle. They are destined to be distributed by blackbirds, jackdaws, and other birds, which devour the hips for the nutriment contained in the fleshy investment; the little nuts, however, pass out undigested in the droppings in some place more or less distant from the Rose-bush. Whilst these birds, attracted by the coloured fruits, are welcome guests, the case is quite the reverse as regards mice and other little rodents; they gnaw the nuts, and devour their contents, the seeds. But the Rose-hips are well-protected against these animals. The stems and branches, up which they must climb to reach the fruits, are provided with sharp prickles with downwardly-directed points, which give complete immunity against these animals. I have repeatedly, in the late autumn, when the mice desert the fields and take up their winter-

quarters in the abode of man, strewed the ground in my garden with Rose-hips of an evening. Invariably, next morning, I found that they had been gnawed and demolished by mice, whilst those remaining *in situ* on the plants were untouched. The fruits of several dwarf Palms are similarly defended against the attacks of animals, by zones of spines upon the stem, prickles upon the floral investments, &c. The berries of several shrubby Solanaceæ (e.g. *Solanum sodomæum*, and *S. sisymbriifolium*) gain a like protection, as do those of the Blackberry, from numerous prickles which clothe the stem and even the fruit-stalk and calyx. In

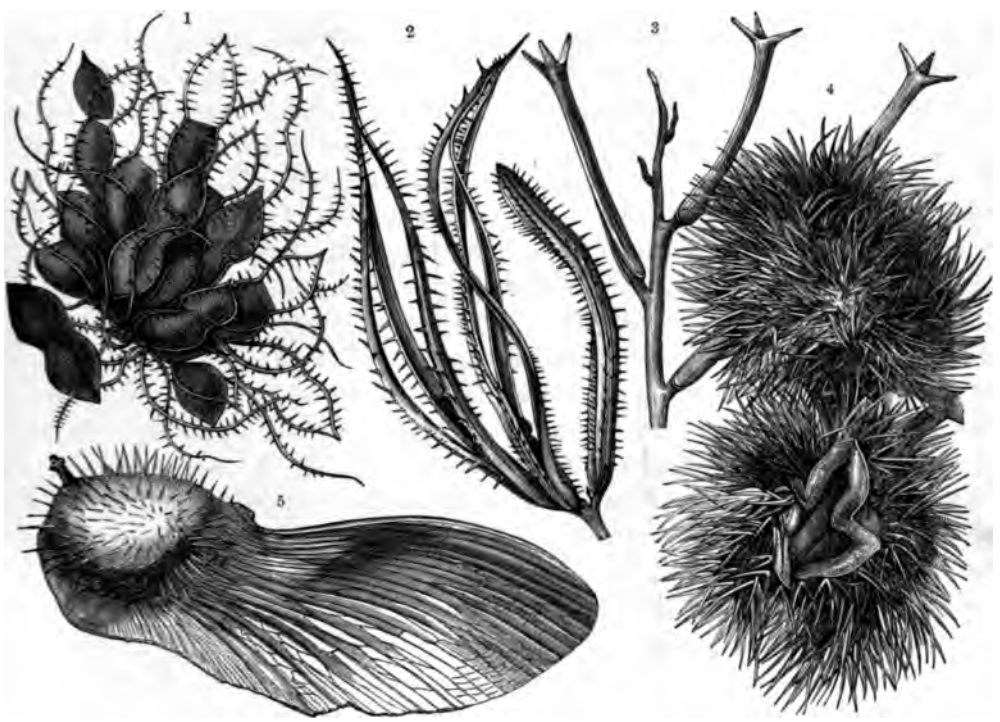

Fig. 339.—Protection of ripening seeds against the attack of animals.

[1] *Mimosa hispidula.* [2] *Schrankia.* [3] *Matthiola tricuspidata.* [4] *Castanea vulgaris.* [5] *Centrolobium robustum.*

several members of the Gorse genus, *Ulex Gallii*, *micranthus*, and *nanus*, the pods are borne upon branches which bristle with spines. The spines project beyond the pods, and their sharp points being directed downwards, mice are prevented from climbing up and working havoc.

Other animals besides these rodents, such as caterpillars, snails, earwigs, centipedes, and the like, have to be warded off. Some caterpillars find the green ovaries acceptable as food, others the seeds themselves. Still, as we have seen, it is of direct advantage to several Caryophyllaceæ, Leguminosæ, and species of *Yucca*, that a portion of the seeds should fall to the lot of insect-larvæ (*cf.* pp. 153–161). It may be repeated here that prickles and spines, the points of which are directed upwards, serve to protect the foliage against browsing animals (*cf.* vol. i. p. 432). In the above-mentioned case of the Gorse, the spines towards the tips of the

branches keep browsing animals away, whilst those inserted lower down, which are directed earthwards, prevent mice from climbing up the plant.

A peculiar protective contrivance has been observed on the calyx of several Labiates, *e.g. Thymus, Calamintha, Ballota.* The corolla falls away after fertilization, but the calyx persists, forming a sheathing envelope for the 4 nutlets. For the better protection of these nutlets the mouth of this cup-like envelope is closed by the development of a crown of hairs, which is impenetrable to small, seed-devouring animals. A further use of these envelopes in seed-dispersal will be alluded to in another place.

In other cases fruits are protected against unwelcome guests, not by spiny structures, but by the elongation of their stalks during ripening, rendering them inaccessible. Thus it would be a difficult feat for a mouse to reach the pendent pods of the Pea (*Pisum*), or those of the Vetches (*Vicia dumetorum, V. pisiformis, V. sylvatica*). Should by any chance a pod be accessible to these animals, by some other route, it is as good as lost, as the nutritious seeds of these plants are much sought after by them. Cherries also, on their long stalks, no doubt derive considerable immunity from earwigs, centipedes, &c., as those which fall to the ground are speedily attacked and devoured.

In the case of seeds whose dispersal depends on the attraction of animals by sweet, fleshy pericarps, these tissues are the reverse of appetizing before they are ripe; not until the seeds are ready to be separated from the parent plant do fruits of this kind become attractive. It is only necessary to cite as instances unripe Cherries, Plums, Apples, and Grapes. It was stated on a previous occasion (vol. i. p. 462), when dealing with chemical changes occurring in plant-tissues, that the fleshy parts of fruits are rendered disagreeable to animals before they are ripe by the presence of bitter or poisonous glucosides, &c. Later on these substances are altered, perhaps under the influence of the acids, which are present in large quantities in unripe fruits, and their place taken by sugars and other harmless materials; thus, what is at first unattractive, and even repulsive, becomes, on ripening, a nutritious food, much sought after by animals, which, at the same time, unconsciously disperse the contained seeds. In this connection the Walnut (*Juglans regia*) is very instructive. Until the seed contained in the "nut" (here really the stone of a drupaceous fruit) is ripe, the latter is surrounded by a fleshy investment rich in tannin. It is not known at this stage that the "nuts" are ever interfered with by nut-crackers or other animals. But on the ripening of the seed the fleshy envelope splits, and the "nut" becomes accessible.

In other cases it is not by acids or bitter stuffs that the seeds are protected, but by strong-scented resinous or sticky substances, which are contained in the cells and passages of the fruit. Thus, in the scales of the cone of the Arolla Pine (*Pinus Cembra*) quantities of resin are present until the seeds are ripe. If the cones be cut with a knife this resin escapes, and can only be removed from the blade with the utmost difficulty. Were a nut-cracker to peck the scales at this stage to obtain the young seeds, its beak would get all besmirched with the resin. It

is easy to observe at Zermatt and Arolla in the Pennine Alps, where this Pine grows, that the nut-crackers attack only the fully-ripened side of even almost ripe cones. As the cone ripens the seeds become easily accessible, but with their manner of dispersal we shall deal in a later section of this work. Here we are concerned only with the fact that many ovaries and fruit-envelopes render their contents undesirable to animals by sticky secretions or disagreeable scents. The pods of several Leguminosæ, *e.g.* species of *Adenocarpus* (*A. decorticans*, *A. Hispanicus*, &c.), are invested both on their flat sides and round the edge with short-stalked, sticky, brown glands, which are to be regarded as a protective arrangement for the young pod. The same obtains in the Hemp (*Cannabis sativa*), though here it is not the ovary but the scales immediately about it which are sticky and strongly odorous. So also in the Hop (*Humulus Lupulus*), the fruits are invested in scales bearing glands which play a like part. Even the ubiquitous sparrow leaves the fruits of these two plants alone during the period of ripening.

Of not less importance to the young embryo is protection against *injurious climatic influences*. Among these, undue moisture and dryness are the chief; and it is to be expected that due provision against them should be made on behalf of the young plant whilst it remains on the parent. Seeds contained in berries, drupes, and indehiscent fruits, as well as those which, produced in capsules, are dispersed at the moment of fruit-dehiscence, hardly come under consideration here, as the opportunities for hurt by weather are relatively small. But in the case of dehiscent fruits which open by means of valves, teeth, or pores, and in which the seeds are retained for some time after the opening of the fruit before they are scattered, provision must be made against the entrance of rain into the cavity of the fruit, which might injure the seeds. This class of danger is averted by the fact that the various valves, teeth, &c., which guard the apertures of the fruits, are very hygroscopic and close in humid weather; or, what is equivalent to this, they only open in dry weather, especially under the influence of drying winds. To make this remarkable contrivance intelligible we must briefly describe the arrangements for seed-dispersal obtaining in capsules of the kind. Capsules opening by valves, teeth, &c., are usually inserted on long stalks, or, if sessile, the axis from which they arise possesses considerable length. These stalks are fairly stiff, and oscillating to and fro in gusts of wind the contained seeds are shaken out, usually as the capsule springs back after the blast. In the case, for instance, of the beaker-like capsules of the Nottingham Catchfly (*Silene nutans*, fig. 340[5]) the seeds cannot fall out of their own accord, the opening being directed upwards; but as soon as the wind sets the long stalk in vibration they are jerked out. For this mode of scattering of the seeds it is essential that the apertures of the fruit should be directed upwards. Indeed, in the great majority of cases of this class, this is their position. In this Catchfly at the time of flowering the flower-stalks are pendent (see figs. 238 and 239, pp. 154 and 155), but, as the fruit ripens, the fruit-stalk becomes erect; the same thing is well shown in the Martagon Lily. On the other hand, when the fruit-stalk bends down after flowering, as in the Bellflower (*Campanula*,

fig. 340[1]) and in the Winter Green (*Pyrola*, fig. 340[6]), the holes and slits are not formed at the apex of the fruit, which is directed downwards, but at its base, close to the insertion of the stalk. This position of the apertures would render the inside of the capsule liable to wetting from rain, &c., and the contained seeds to injury therefrom, were it not for the fact the openings are closed when this danger threatens. The wall of the capsule is very hygroscopic, and the slits and valves quickly close in damp weather. In fig. 340 several examples of this opening and

Fig. 340.—Protection of seeds against wet.

[1] Capsules of *Campanula rapunculoides* in dry, [1'] in wet weather. [2] Capsule of *Lychnis diurna* in dry, [2'] in wet weather. [3] Capsules of *Linaria Macedonica* in dry, [3'] in wet weather. [4] Capsules of *Cerastium macrocarpum* in dry, [4'] in wet weather. [5] Capsules of *Silene nutans* in dry, [5'] in wet weather. [6] Capsules of *Pyrola chlorantha* in dry, [6'] in wet weather. [7] Capsules of *Gymnadenia Conopsea* in dry, [7'] in wet weather. [8] Capsule of *Pinguicula vulgaris* in dry, [8'] in wet weather.

closing are represented. In the already mentioned capsule of the Catchfly (fig. 340[5]) the aperture at the summit is guarded by a number of divergent teeth; the same is true in the case of those of various species of Toadflax (e.g. *Linaria Macedonica*, fig. 340[3]). In *Cerastium macrocarpum* (fig. 340[4]) the opening is directed laterally, and in the Campion (*Lychnis diurna*, fig. 340[2]) the capsule is erect with revolute teeth. In the Bellflower (e.g. *Campanula rapunculoides*, fig. 340[1]) small, circumscribed portions of the wall near the base fold back as valves, giving rise to as many apertures; in the Winter Greens (e.g. *Pyrola chlorantha*, fig. 340[6]) a number

of slits arise near the base, while in the Butterwort (*Pinguicula vulgaris*, fig. 340[8]) the fruit splits into two valves. How all these capsules behave is shown in the portion of the illustration with the shaded background (figs. 340[1'] to 340[8']). Closure is so complete that the entrance of moisture into the capsules is impossible, and the seeds have absolute immunity from premature wetting. Even in the case of capsules with lateral slits, where there is a possibility of moisture entering, the same arrangement prevails, as is well illustrated in the Fragrant Orchis (*Gymnadenia Conopsea*, *cf.* figs. 340[7] and 340[7']).

Of capsules with openings directed downwards there are but few, and in these the dispersal of the seeds is not accomplished quite in the same manner as in those just described. In the Funkias (*Funkia ovata, Sieboldi, subcordata*, &c.) the pendent capsules open by three valves at their depressed tips, and concurrently some of the seeds are shot out into the air—often to some little distance. Those which remain in the capsule after the sudden opening are not, as one might expect, deposited in a heap on the ground close by, but, being attached to the valves by delicate strings, and having a flattened form, offer considerable surface to the wind, which ultimately loosens them and bears them far away. The fact should be emphasized that in many cases fruits only open under the influence of dry winds, and that the same wind which promotes their dehiscence at the same moment scatters the seeds. This is very well shown by the Scotch Pine (*Pinus sylvestris*). Its cones only separate their scales in the afternoon when the air is driest and a wind is blowing. When the conditions for this are favourable one hears quite a series of noises in the tree-top, caused by the separating of the scales, and at the same time the winged seeds go spinning through the air. The scales protect the seeds in this case against wetting, and indeed against other dangers as well. It should be remembered that any protective arrangement is but rarely directed solely against one particular source of danger. An envelope may protect the embryo at one time against the wet, at another against excessive desiccation; sometimes the same envelope may also ward off attacks from undesired guests of the animal world.

Developments on fruits whose chief function is the protection of the seeds against *desiccation* are, on the whole, scarce. In certain portions of Australia the whole vegetation enters upon a sort of summer sleep; during this period no rain falls and the surface of the earth is hardly ever wetted with dew; such a dryness of the air and of the soil prevails that plants are compelled to suspend operations for a while. It has been already explained how the foliage is protected against drying up (*cf.* vol. i. p. 296); but the embryo also, which has arisen within the ovule during the period of vegetative activity, has to be preserved during this period. This is achieved by the massive development of the ovary wall, which in this respect exceeds anything met with in the Floras of other regions of the globe. The seeds of the Wooden Pear (*Xylomelum pyriforme*, see fig. 325[2] p. 431) are inclosed in a strong pericarp, the wall of which attains a diameter of 2 centimetres, and can resist the greatest dryness for very long periods. So also is it with the seeds of the Australian species of *Banksia* and *Eucalyptus* (see figs. 324 and 325 [13, 14] pp. 429

and 431), the walls of their capsules being exceedingly thick and strong. In not a few Steppe-plants the seeds within are protected by the nature of the inclosing pericarp during the hot, rainless summer season. Remarkable amongst them are the big Umbelliferous genera *Prangos* and *Cachrys*, the schizocarps of which are protected by a thick spongy wall not unlike elder-pith in nature. Preserved within these walls against desiccation, the embryo secures this further advantage, that from the relative largeness and lightness of the fruits they are readily dispersed by the wind over the Steppe.

In dry, dehiscent fruits protection against unfavourable climatic conditions is extended only so long as the seeds remain attached to the parent plant; in achenes, nuts, and schizocarps it lasts longer, however. For in the latter classes of fruit the pericarp accompanies the seed after severance, protecting and aiding it during its passage, and often assisting it at germination. All those developments of the seed-coat, met with in the cases in which the seeds themselves are liberated, are replaced, in these non-dehiscent fruits, by the pericarp or other associated portion—calyx, bracts, and the like. These structures are fashioned so as at once to preserve the seed on its journey, be it by air or water, and to attach it to its germinating-bed by various irregularities of surface—pits, furrows, warts, or even sticky excretions. Further, it is important that arrangements be provided so that the young plant should have access to water at certain spots on the fruit wall, and that on germination it should be able to push out its young rootlet without undue effort, as, for instance, in the Water-chestnut and Bulrush (*cf.* vol. i. p. 607, figs. 144 [3, 4, 11, 12, 13]).

The stage of development at which the embryo is detached from the parent plant is not the same in all cases. In the Maidenhair Tree (*Ginkgo biloba*) the embryo is but slightly differentiated at the time when the plum-like seed falls. The egg-cell has been already fertilized, and the enveloping tissues of the seed have matured, but the differentiation of the embryo is postponed till after the seed has fallen. So, too, in Orchids and in many parasitic and saprophytic plants, such as *Cuscuta*, *Orobanche*, *Monotropa*, and Balanophoreæ, the embryo, at the moment of severance of the seed, is of the most rudimentary character. But in the majority of Phanerogams the embryo shows a differentiation into plumule, and radicle, and cotyledons. In *Ceratophyllum* the plumule has already slightly elongated and exhibits a number of little leaves, and in *Nelumbium* the leaves show a differentiation into blade and petiole. In the Mangrove Tree (*Rhizophora Mangle*, see fig. 341 [1]) the embryo attains to a very considerable degree of development whilst still attached to the parent plant. Its root penetrates the wall of the ovary (fig. 341 [2]) and ultimately attains a length of 30–50 cm. and a thickness of 1–5 cm. and a weight of some 80 grams. Finally, the young plant breaks away from its sucker-like cotyledon and falls into the mud below, where it speedily unfolds a pair of green foliage-leaves (*cf.* vol. i. p. 604). Thus, in the Mangrove Tree, it is not the seed but the embryo which is detached from the parent plant. Comparing the *Ginkgo* to an oviparous animal, the Mangrove might be regarded as viviparous.

The envelopes which surround the embryo at the moment of detachment vary

enormously from plant to plant. The seed of the terrestrial Orchid *Gymnadenia*

Fig. 341.—Mangrove Tree (*Rhizophora Mangle*).

[1] Branch with flowers and fruits (reduced). [2] Single fruit, the apex of which is being penetrated by the radicle of the embryo. (After Baillon.)

Conopsea measures 1 mm. in length and weighs ·008 gram: that of the Cocoa-nut Palm 11--14 cm. and weighs 800–1100 grams. The Wind Bent-grass (*Apera spica-*

venti) has a grain 1·2 mm. long, ·3 mm. broad, and weighs ·05 grm.; the fruit of the Seychelles Palm (*Lodoicea Sechellarum*) measures 32 cm. by 18–25 cm. by 22 cm., and weighs 4200–4800 grams. The largest fruits are produced by the Cucurbitaceæ; in a suitable soil Gourds attain a diameter of half a metre, whilst fruits of the Melon-pumpkin (*Cucurbita maxima*) have a greatest diameter of over a metre, and a weight of 75 to 100 kilograms. The fruits of the Bottle-gourd (*Lagenaria*) attain under favourable circumstances a diameter of 30 cm. and a length of a metre and a half.

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3. CHANGE IN REPRODUCTIVE METHODS.

Fruits replaced by Offshoots.—Parthenogenesis.—Heteromorphism and Alternation of Generations.

FRUITS REPLACED BY OFFSHOOTS.

By *Annual Plants* are understood such as germinate, grow, and conclude their flowering and fruiting within the limits of a single year, and after the ripening of their seeds die away. The activity of these plants is concentrated on the production of a large amount of seed; it is worthy of note that autogamy is frequently met with amongst them, followed by good results. They produce just so many foliage-leaves as are necessary to provide the materials for their flowers and fruits, and reserve-substances for their seeds. With the production of seed, the leaves, stems, and roots perish without forming vegetative buds or offshoots, so that these plants are represented for several months by their seed only. Their rejuvenescence can only occur under favourable climatic conditions where an unimpeded germination is allowed these seeds, and when no interference in the process of development is imposed by men or animals. If the weather be unfavourable in the situations where the plants have established themselves, if the summer be a cold one, so that fruit cannot be ripened, they do not perish at the end of the first year, but prolong their existence till another year by means of offshoots, becoming, for the time being, perennial plants. We may put it, in a manner of speaking, that when the danger of extinction threatens, fruit-production is replaced by offshoots; instead of fruits, tubers, buds, or other shoots are produced, and not infrequently these structures arise in the position usually occupied by fruits. Among the Crassulaceæ there are several annual species (*Sedum annuum, glaucum*, &c.) which normally die away so soon as their seeds have ripened and been dispersed. But when it happens from any cause—as by the premature on-coming of winter—that these processes are interfered with, little rosettes of leaves arise from the base of the stem in close proximity to the root; these are detached, and, as offshoots, continue the life of the plant into another season. Similar phenomena are observed in many other herbs whose flowers or fruit are destroyed by frost. Indeed by experiment these statements can be readily verified. Members of various families (*Poa annua, Senecio nebro-*

densis, S. vulgaris, Ajuga Chamæpitys, Herniaria glabra, Viola tricolor, Cardamine hirsuta, Medicago lupulina), normally annual, are transformed into perennial plants when grown in my alpine experimental garden on the Blaser in Tyrol (Gschnitzthal), at a height of 2200 metres, there being insufficient warmth there for them to produce good seed.

Interference with fruit-production due, in inhospitable situations, to an unfavourable climate, can be artificially brought about by the removal of the flowers from a plant as they appear. Annual plants pruned in this way produce shoots and offshoots which would otherwise have remained undeveloped. These remain living till next year, and if the same treatment be continued indefinitely, a plant, otherwise annual or biennial, becomes perennial. Upon this fact depends the gardening feat of producing little Mignonette trees. Normally the seeds of this plant germinate in a sandy and humous soil, and the plants arising perish in the autumn after flowering and ripening their fruit; but if the inflorescences be carefully pinched off, the stem doesn't die down but produces lateral shoots with the object of developing new flowers. If these flowers be removed year after year, gradually a little tree is formed, with woody stem and branches; and if ultimately it be left alone will cover itself with hundreds of sweet-scented flower-spikes. That a much increased production of leafy shoots and offshoots can be stimulated in perennial plants by this kind of pruning has long been known; by its aid many modes of propagation, as practised in horticulture and agriculture upon cultivated plants, are obtained.

It sometimes happens in nature that a failure of flowers is due to the plants being overshaded. That is to say, many plants growing in shady places either do not produce flowers or their flower-buds do not open and cannot ripen fruit. Such plants produce offshoots from the lower portion of their stem in the form of leafy shoots, runners, &c., if they are able to do so, and this in a very marked degree; in other words, the more flowering and fruit-production is hindered by shading, the more is a development of offshoots promoted. The Willow-herb (*Epilobium angustifolium*) develops its beautiful flowers only in sunny situations, accessible to hive- and humble-bees. The more intense the sunlight, the more vividly are the flowers coloured. Should trees grow up and densely overshadow the Willow-herbs, the flower-buds atrophy before opening and fall away from the axis as small withered structures. Whilst the richly-flowering plants form only short offshoots, these shaded plants produce long, subterranean runners, which seek to penetrate to a distance, out of the circle of shade.

Another remarkable phenomenon in the growth of perennial plants, which flower and fruit copiously under favourable climatic conditions, is that in inhospitable situations, where this is restricted, they propagate themselves very readily by means of offshoots. A Composite, *Nardosmia frigida*, allied to the Butter-bur, is widely distributed over the Arctic regions. Only towards its southern limits does it produce flower and fruit; further north flowers are never met with upon it, but, instead, it propagates itself far and wide by means of

offshoots. Similar in its behaviour is another Composite, the alpine *Adenostyles Cacaliæ*. It blossoms and fruits in sub-alpine forests even up to the tree limit, but in high alpine regions, above 2200 metres in altitude, it never flowers, but forms offshoots, and in this way fills little depressions on alpine slopes with its vigorous foliage. The terrestrial form of *Polygonum amphibium* occurs in a little bog close to my country house in the Gschnitzthal in the Tyrol at a height of 1200 metres. For twenty-eight years I have examined this bog every year without ever finding a ripe fruit upon these plants. But it propagates itself with rare luxuriance by means of offshoots and forms a broad girdle around the bog. These plants, *Nardosmia frigida*, *Adenostyles Cacaliæ*, and *Polygonum amphibium*, grown in a more favourable climate, produce good seed, but their vegetative methods of propagation are so restricted that one might almost suppose them to be different species of plants.

Instances in which flowers are replaced by offshoots or bulbils in the inflorescence may be mentioned in connection with the above. *Polygonum viviparum* and *bulbiferum*, *Saxifraga cernua*, *nivalis*, and *stellaris*, *Juncus alpinus* and *supinus*, and the Grasses *Aira alpina*, *Festuca alpina* and *rupicaprina*, *Poa alpina* and *cenisia* occur, it is true, with normally developed flowers and fruits, but in alpine, and especially in arctic regions, where these plants have their head-quarters, one very frequently finds purely vegetative buds or bulbils, which become detached from the parent plant and give rise to new individuals, in place of flowers and fruit. In the Polygonums mentioned little bulbils replace a portion of the flowers. *Saxifraga cernua* usually produces a single terminal flower at the end of its inflorescence, the lateral flowers being replaced by little tufts of bud-like offshoots on short stalks (see fig. 342 [8]). These buds, when they fall off, are either still closed (fig. 342 [5]), or their thick, fleshy, outer scales are already parted, exposing a little green foliage-leaf. On the ground they soon produce roots and grow into new plants (see figs. 342 [6] and 342 [7]). In *Saxifraga nivalis* little shoots are formed in place of flowers, each bearing a tuft-like rosette of minute leaves (fig. 342 [1]). These rosettes are readily separable, and producing roots from their abbreviated axes, give rise to new plants. So also in the Juncuses and Grasses mentioned, little shoots replace the fruits and come away from the inflorescence. These shoots are produced in *Poa alpina* (see fig. 342 [8]) and in most of the other Grasses mentioned, in the following manner. The axis of each spikelet, after producing several glumes at its base, forms green leaves above—as it were a grass-plant in miniature (see figs. 342 [9] and 342 [10]). Later, these disarticulate, take root, and grow into new plants. More rarely do shoots arise laterally on the axis, in the axils of subtending scales; when this is the case they fall away in the usual manner. The earlier Botanists termed all such Grasses, and indeed all plants which produce bulbils in their inflorescences, *viviparous*, the idea being, that in all of them the seeds germinated precociously whilst still attached to the parent. This view was probably suggested by the common experience of agriculturalists that Rye, Oats, and other cereals sometimes "sprout", *i.e.* that when the spikes are continually wetted by rain about

the time of harvest, and the haulm laid flat on the ground, the embryos begin to develop whilst the grain is still in the ear. This premature germination, however, is quite independent of the parent plant, which has given up all its food-materials, and is already dead; the grains, held between the glumes mechanically, are no longer in vital connection with the plant which gave them origin. Their germination between the damp husks is similar to what would occur between pieces of moist blotting-paper. But in these so-called "viviparous plants" the phenomenon

Fig. 342.—Bulbils replacing flowers and fruits.

[1] *Saxifraga nivalis* with rosettes of little green leaves instead of flowers (natural size). [2] Two of these rosettes, enlarged; one of these has become detached from its stalk. [3] *Saxifraga cernua* (natural size). [4] A cluster of bulbils of this plant. [5, 6, 7] Bulbils of same in various stages of development. [8] *Poa alpina* with bulbils replacing its flowers (natural size). [9] A portion of the inflorescence (enlarged). [10] A miniature grass-plant developed between the glumes of a spikelet of *Poa alpina* (enlarged).

is quite different from this "sprouting" of cereals. In them no flowers or seeds are formed, consequently there can be no germination of seeds still united to the parent plant. The detached structures, formerly regarded as germinated seedlings, are in reality little, leafy shoots which have been produced instead of flowers and fruits.

The plants which we have just been discussing are essentially forms living in high alpine and arctic regions, that is to say, in regions in which they have but some two to four brief months in the year in which to complete their vital processes. In the majority of plants growing under such inhospitable conditions,

the flowers for the following summer are already developed in miniature the preceding autumn, so that on the melting of the snow and the termination of winter the flowers can be at once expanded. When such plants can avail themselves of the warmth of the whole summer they are able to ripen fruit and seed. But it is otherwise with those which produce their flowers on a leafy axis, and which must first form an under-structure on which they can be produced; with these, before flowers can be unfolded, a considerable interval of time must elapse. Their blossoming is delayed, and the ripening of their seed takes place quite at the end of the period of vegetation. There is thus always the danger of early frosts or of the winter-covering of snow intervening before the seeds can be ripened and dispersed. It is in just such plants that preservation and propagation are ensured by a development of bulbils; these structures are more speedily produced than seeds, nor do they require so much warmth; further, they are not so liable to injury from premature advent of winter as are developing fruits. The above-mentioned Polygonums, Saxifrages, Rushes, and Grasses are amongst those which flower relatively late, and are liable, in unfavourable seasons, to a destruction of their seeds. The very frequent substitution in them of vegetative for sexual reproduction would seem to be undoubtedly correlated with this liability of seed to fail. And in not a few steppe-plants the substitution of offshoots for flowers is probably connected with the fact that with them, also, the season is not always long enough for the formation of stem, flowers, and fruit.

It has been previously pointed out that a great many aquatic plants, with roots fixed in the mud and stems and foliage floating in the water, raise their flowers above the surface and avail themselves of the wind and of flying insects for pollination and fertilization. For such plants fluctuations in the level of water must be of considerable moment, and it may well be that if the surface is raised for any length of time, flowering and fruiting are hampered, and, in many cases, rendered impossible. Many marsh and water plants possess, indeed, the capacity of stretching to the surface, the stem continually elongating as the level is raised, until the flowers can be expanded above the surface. But this growth in length has its limits, and it not infrequently happens that, even after an extraordinary elongation of stem and flower-stalk, the surface of the water is not attained. And these flowers in most cases cannot be fertilized under water; if already formed, the flower-buds do not open, but atrophy and fall off without producing fruits. In the little meres of the Black Forest, *Littorella lacustris*, a plant allied to the Plantain, grows; but it only flowers and fruits in very dry years, when the expanse of water is much contracted and the bottom is in large part laid bare. But this is not very often; ten years may pass without the conditions favourable to the flowering and fruiting of *Littorella* obtaining. During the whole of this time the plant must remain barren were it not for the fact that off-shoots, which take root in the mud, are produced instead of fruits. Thus it is able to maintain and propagate itself. Several Pondweeds and Water-crowfoots (*Potamogeton* and *Ranunculus*) behave

like *Littorella*, and it would appear that the capacity to propagate by offshoots, so common in aquatic plants, is connected with the impediment to flowering so often presented by a high water-level. *Cymodocea antarctica*, a submerged aquatic plant, which grows in great luxuriance on some parts of the coast of Australia, flowers so rarely that its peculiarly formed bulbils were for a long time regarded as its flowers. Nor has every Botanist seen the flowers and fruits of the Duckweed (*Lemna*); whilst the renowned American Water-weed, *Elodea canadensis*, which has been such an obstacle to navigation in canals, &c., but seldom flowers, and owes its very remarkable propagation and distribution, not to fruits, but to a quick and plentiful production of offshoots.

A dearth of water, also, like a too ample supply, can render fertilization impossible and promote the propagation and distribution of some plants by offshoots to a remarkable degree. In Ferns and Mosses the spermatozoids reach the archegonia, swimming in the water which accumulates on or about the sexual generation of these plants (*cf.* pp. 65 and 68). In the great majority of cases, it is rain and dew which provide the capillary water which invests the plants, and in which the spermatozoids swim. And other conditions in the life of Ferns and Mosses besides fertilization depend on an adequate supply of water; their existence depends on a certain definite amount and on a certain annual duration of atmospheric precipitation. Mosses, and particularly Ferns, have but a restricted distribution in dry localities; or they may be entirely wanting. In humid regions, on the other hand, they attain to a luxuriant growth. The contrast in this respect is striking enough for illustration. Elvend Kuh, a mountain in the interior of Persia, rises to a height of some 3750 metres, and is the culminating point of a considerable plateau. The rainy season is limited to a period of two months, and a rich and well-marked steppe-flora covers the ground. Ferns are absent from an area some 5000 square kilometres in extent, whilst Mosses are only represented by a few species which propagate by means of thallidia, rarely maturing spore-capsules. In the hill country of the West Indies, particularly the Blue Mountains of Jamaica, the vapour condenses every morning, and in the course of the afternoon is precipitated as rain. Here are found some 500 Ferns, and large numbers of Mosses and Liverworts. The level or sloping ground, rocks, the forest floor and decaying tree-trunks, all are covered with Ferns of every shape and size; there are groves of Tree-ferns, the trunks of trees are invested right up to the crown with delicate, green fronds, whilst tiny representatives of the Filmy Ferns (Hymenophyllaceæ) have actually taken up their abode on the foliage-leaves themselves. Within a distance of a hundred paces the plant-collector can find fifty different sorts of Ferns, and as many Mosses.

And between the extremes we have described there are regions with an intermediate climate, of such a character, that although the fertilization of Ferns and Mosses is not perpetually prevented, still wet years are rare, and several years may elapse without the conditions being favourable for it. Such a region is the Hungarian plains, the fields and woods of which produce only two species of Ferns and

some dozen Mosses. The latter have almost entirely ceased developing fruits, and propagate themselves for the most part by thallidia, since these can be produced much more simply, and their production is independent of enduring drought.

Certain Ferns must be mentioned in this connection, on the prothallia of which offshoots arise instead of normal, sexually produced embryos. It is true that they form archegonia, but they are abortive, and propagation is asexual. The little Fern-plant arises not from the archegonium but from the tissue in its immediate neighbourhood; the archegonia remain closed, are not fertilized, turn brown, and die. This substitution may be observed in *Aspidium falcatum*, in a crested variety of *Nephrodium Filix-mas*, and in the variegated form of *Pteris Cretica*, frequently cultivated in greenhouses. On the prothallia of normal forms of *Nephrodium Filix-mas*, and on those of wild plants of *Pteris Cretica*, fertilization takes place in the usual way, so that it is possible that the substitution of offshoots for fruits is a result of the conditions of cultivation. To what causes exactly the phenomenon in question may be due, is, however, unknown.

As factors in promoting a substitution of offshoots for fruits amongst the Mosses, other climatic conditions exert considerable influence. But it would lead us too far were we to treat of all these in detail; only a few of the fifty or so examples from the European Moss-flora can be mentioned here. *Leucodon sciuroides*, a Moss which rarely fruits in Northern Europe, produces instead numerous leafy shoots (brood-bodies) which, becoming detached, readily root on a moist substratum (see figs. 196 [9] and 196 [10], p. 23). *Campylopus fragilis*, again, scarcely ever produces fruits in the Alps; it forms readily separable lateral branches, the leaves of which are carried away by the wind. Any of these leaves falling on a moist spot develops green filaments, upon which little buds arise, originating new leafy Moss-stems (see fig. 196 [11], p. 23). The case of *Barbula fragilis* and *Timmia Norvegica*, growing in the Alps, is similar to that of *Campylopus*. Of several Mosses the fruits have never been seen; such are *Dicranodontium aristatum*, *Barbula papillosa*, *Grimmia torquata*, *Bryum concinnatum*, and *B. Reyeri*. They are able to maintain themselves in spite of this by vegetative propagation.

In addition to the cases already enumerated, in which climatic conditions, excess or lack of water, &c., promote vegetative as opposed to sexual reproduction, numerous others are known in which peculiarities in the structure of the flowers cause the ovaries to abort, or make it necessary that a formation of offshoots should be initiated if the plants are to be maintained. In this connection certain hybrid Fuller's Thistles and Mulleins (*Cirsium* and *Verbascum*) must be noted. The plants in question are hybrids, that is to say, they are produced by crossing of different species. They flower early in the summer, and have ample time to ripen seed before the on-coming of winter, but in a number of these hybrids, owing to variations in the structure of the flowers and of the pollen, few or no seeds are ripened. On the other hand, just these very plants form aërial buds and subterranean offshoots very freely. *Cirsium purpureum*, a hybrid between

Cirsium heterophyllum and *spinosissimum*, and *Cirsium affine*, a hybrid between *C. heterophyllum* and *C. oleraceum*, are very abundant in many Alpine valleys, and one may find more examples of these hybrids than of their parents in many a meadow. Several of the Fuller's Thistle hybrids, the parents of which are biennial, become perennial by a production of lateral shoots from the leaf-axils at the base of the stem. Here also, as with climatic conditions, we find vegetative propagation replacing fruit-production.

There are also many species, of which it cannot be definitely asserted that they have arisen by hybridization in recent times, which fruit but seldom even when the climatic conditions are in every way favourable for this kind of reproduction. According to agriculturists, there are many kinds of Potato which flower only occasionally but do not ripen fruit, although the flowers and pollen-grains appear quite normal. It is just these Potatoes which are characterized by their rich production of tubers, fruit-formation being in them replaced by vegetative propagation.

That plants, with double flowers, the ovaries of which, under the influence of little insects (*Phytopus*), have undergone a deep-reaching transformation, should ripen no fruits is to be expected and has long been known, as also is the fact that these plants produce buds and offshoots freely. Of special note in this connection is a Bitter-cress (*Cardamine uliginosa*) often met with in damp meadows in the neighbourhood of Vienna, Salzburg, and Ried, growing wild with double flowers. On most of the plants, the fruits of which are abortive, those curious leaf-buds, represented in fig. 200 [4], p. 41, are to be found.

Again, with many species of plants, it may come to pass that the insects which should accomplish their pollination are now no longer prevalent in the region where the plants grow, or indeed have entirely deserted them. This category of plants obviously includes only such forms as are destitute of arrangements for promoting autogamy, in the case of cross-pollination not taking place. In a very considerable number of these plants, flowers and fruits are replaced by offshoots—offshoots of the most varied kinds, including aërial and subterranean tubers, bulbils, green leafy shoots, and, in rare cases, little bud-like structures, from each of which a thick, fleshy root arises in such a manner that the greater part of the offshoot consists of a root.

As all these varieties of offshoots will be dealt with in a later chapter devoted to the distribution of such structures by wind, animals, and special mechanisms, it must suffice to speak here of a very few cases. Growing in sunny spots, the yellow flowers of the Lesser Celandine (*Ranunculus Ficaria*) are occasionally visited by little pollen-eating beetles, by flies and bees; under these circumstances heads of fruit are ripened here and there from the flowers. But in shady places, beneath bushes, and on the dark forest floor, these insect-visits are much rarer, and almost all the flowers fail to ripen fruit. These shaded plants, however, develop little bulbous bodies in the axils of their upper foliage-leaves, which become detached on the withering of the shoot and give rise to new plants (see

fig. 343[3]). Those which ripen fruit, on the other hand, form no offshoots, or only very few. In the Coral-root (*Dentaria bulbifera*, see figs. 344[1, 2, 3, 4, 5]) a similar state of affairs prevails. Pollination is accomplished only by insect-agency, and where insects fail no fruits are ripened. The plant grows sometimes near the sunny border of young Beech-plantations where insects are plentiful, and also in the forest of older growth in whose dusky glades bees and flies, humble-bees and butterflies are rarely met with. Those which grow in the better lighted, younger

Fig. 343.—Flowers and fruits replaced by tubers and bud-like offshoots.

[1] *Gagea Persica*. [2] *Lycopodium Selago*. [3] *Ranunculus Ficaria*. [4] Bud-like offshoot from the leaf-axil of *Gagea Persica*. [5] Bud-like offshoot of *Lycopodium Selago*. [6] Tuber-like offshoot of *Ranunculus Ficaria*. 1, 2, 3 nat. size; 4, 5, 6 enlarged.

portion of the wood ripen their cruciferous capsules, but the others, in the deep gloom, are free of insects and blossom in vain. Their ovaries for the most part abort and fall away, and only occasionally do their fruits come to maturity (*cf.* fig. 344[2]). But in proportion as fruit-production is arrested, vegetative propagation by bulbils is promoted; large bulb-like buds are formed in the leaf-axils, which disarticulate as summer advances and the shoot begins to fade; they are detached by the wind as it sways the stems, and falling on the moist floor of the forest take root (fig 344[4]) and give rise to subterranean rhizomes (fig. 344[5]). Some plants

occur in these shady spots which bear no flowers at all, and depend entirely on a production of these offshoots (*cf.* fig 344[3]).

There are two forms of Orange Lily indigenous to Europe. One (*Lilium croceum*), occurring especially in the Pyrenees and South of France, almost always ripens fruits and forms no bulbils in its leaf-axils. The other (*Lilium bulbiferum*),

Fig. 344.—Flowers and fruits replaced by bulbils. The Coral-root (*Dentaria bulbifera*).

[1] Inflorescence. [2] Leafy shoot on which two fruits have ripened; bulbils in the axils of some of the leaves. [3] Leafy shoot whose inflorescence has atrophied; bulbils in the axils of all the leaves. [4] Detached bulbils forming roots. [5] Rhizome of *Dentaria bulbifera*.

found in the valleys of the Central and Northern Alps, hardly ever fruits, but is characterized by the bulbils it produces in the axils of its leaves; bulbils which disarticulate in autumn and are scattered by the wind. But there is no difference noticeable in the structure of the flowers in these two Orange Lilies, and it is difficult to explain their difference in mode of propagation, save on the assumption

that in the regions where *Lilium bulbiferum* grows those insects are wanting which should convey its pollen from flower to flower. As the Orange Lily possesses no arrangements for autogamy, no fruits are formed in the absence of insect-visits. It appears that this plant has lost the capacity for autogamy; at any rate if a stigma be pollinated with pollen from the same flower, on plants in a garden, no result follows. On the other hand, offshoots in the form of numerous bulbils are produced by *Lilium bulbiferum*, by means of which it is propagated and dispersed. In several valleys of the Central Alps it does not flower at all, and thus obviously depends entirely upon its bulbils for propagation.

Gagea Persica (fig. 343[1]) a member of the Liliaceæ, repeats several of the peculiarities met with in the Orange Lilies. The stem of this little bulbous plant terminates in a flower which, in the absence of insect-visits, withers without setting fruit. Little buds arise in the axils of its filamentous foliage-leaves. With the atrophy of its fruits these grow into little bulbils (fig. 343[4]); but if fruit be formed these buds for the most part atrophy. Nor must we omit to mention the ally of this plant, *Gagea Bohemica*, belonging to the flora of Central Europe. From its specific name, *Bohemica*, it might be supposed that it is solely met with in Bohemia; this is not so, it was first discovered there, but is distributed widely over Persia, Asia Minor, Southern Russia, and the Balkan Peninsula. Further west *Gagea Bohemica* occurs rather sparingly, in Bohemia and in the neighbourhood of Magdeburg—these occasional occurrences being no doubt a last lingering remnant of a Steppe-flora which at some former period extended to the Harz Mountains. We shall later have opportunity of explaining how this Steppe-flora has retreated eastwards and been replaced by other communities of plants; here we may mention that this retreat of the Steppe-flora was accompanied by a retreat of the Steppe-fauna. The Steppe-antelope, Steppe-marmot, Steppe-porcupine, rat-hare, &c., which existed in those times in Central Germany, have long forsaken this region, and we have good grounds for assuming that the insects of that period have also migrated. It is certainly remarkable that this Steppe-plant, *Gagea Bohemica*, the flowers of which are adapted to insect-pollination, and in which autogamy does not occur, should never ripen its fruit and seeds in these scattered localities of Bohemia and Germany. One can hardly help supposing that this abortion of fruits is due to the absence of those Steppe-insects which were formerly, in all probability, distributed also over Bohemia and Germany. Whatever be the explanation, it is a fact that these isolated western representatives have never been known to ripen fruit and seed. But instead, at the bases of the leaves, bulbils are formed which fall away and root, maintaining and propagating the species.

Equally instructive is the case of one of the Chickweeds, *Stellaria bulbosa*, now confined to a restricted area in Carniola and Croatia. It flourishes there in the deep, black humus of the forest floor, preferably on the banks of little water-courses, forming here and there dense, luxuriant masses. Its flowers unfold quite early in the spring; and although they are fairly conspicuous, standing up white from the green background, they are rarely visited by insects. The few flies which come to

them seem to be undesired guests; they promote no pollination, and fruits are not ripened. I have sought vainly for fruits in the neighbourhood of Laibach in Carniola where *Stellaria bulbosa* is very abundant; there were thousands of faded flowers, but never a fruit with ripened seeds. Its filamentous subterranean stems, on the other hand, bear innumerable white buds; and if one digs up a handful of the black woodland mould, it simply teems with these offshoots. The little streams in spate after a thunderstorm often wash away some of the humus from their banks, exposing and carrying away these little buds in the whirl of waters. Ultimately they are left somewhere, high and dry; and if the conditions are favourable, take root and establish themselves in these new localities. In this manner, at the present time, is *Stellaria bulbosa* propagated and distributed. We cannot suppose things have always been thus; we are driven to the conclusion that in this case, also, the plant, much restricted as to its distribution, is a fragment of a vanished flora. In the Karst district of Carniola and Croatia such fragments are not infrequent, and when one puts all the facts together one may well conclude that this flora has retreated or been driven back in a south-easterly direction at a period not very remote from our own. Accompanying these changes there may well have been changes in the distribution of the insect-fauna, and those insects which formerly visited the now rare *Stellaria bulbosa* of the Karst, and were of great importance to it, may have migrated eastwards or indeed have become extinct.

PARTHENOGENESIS.

At the commencement of the Nineteenth Century the attention of Botanists was directed to a certain aquatic plant, widely distributed in the Old World from Ireland to China, and from Finland to Northern Africa, and occurring very commonly on the Baltic littoral and its islands. This plant was *Chara crinita*, one of the Characeæ, which flourishes in brackish water near the sea, and here and there in salty, stagnant inland lakes. In whatever ditch or pool it takes up its abode it occurs in large quantities, and forms, like many of its allies, extensive and luxuriant masses. It is an annual plant, dying off in the autumn. Next spring young plants arise from the oogonia which have passed the winter on the muddy bottom—and so from year to year. *Chara crinita* is dicœcious, that is to say, some plants bear oogonia only, others antheridia (*cf.* p. 62). Whilst in the generality of dicœcious Characeæ the male and female plants grow in one another's immediate vicinity, in *Chara crinita* such a distribution is extremely rare. Hitherto, male plants have only been found at Courthezon, near Avignon, in the South of France; near Gurjew on the Caspian Sea; and at Salzburg, near Hermannstadt, in Siebenbürgen (Hungary). I have myself found plants bearing antheridia in some little salty pools near Soroksar, south of Buda-Pesth in Hungary. In the North of Germany on the shores of the Baltic, where *Chara crinita* is very abundant, a male plant has never been found. Nor have Botanists been wanting in their endeavours to find such, should any occur in this region. The Dassower See near

Lübeck, the neighbourhood of Warnemünde near Rostock, the two Jasmunder Boddens (inland branches of the sea), on the island of Rügen, and the Wanger Wieck near Stralsund, where *Chara crinita* is exceedingly plentiful, have been repeatedly searched for male plants but in vain. And the female plants also have been examined in case, perchance, an occasional antheridium might occur upon them, as in the monœcious species of *Chara*. Thus we may take it as established that in the Baltic region no antheridia and consequently no spermatozoids are developed. Nor was the attempt successful to explain the matter on the supposition that at the time of fruiting spermatozoids were brought by water-birds from Hungary, the Caspian, or the South of France. In the Baltic the egg-cells of *Chara crinita* remain unfertilized in their oogonia; the latter fall off in autumn and, without stimulus from any spermatozoid, germinate in the spring. We have here an instance of what Zoologists have termed *Parthenogenesis*. It has been demonstrated with certainty that new individuals arise from unfertilized eggs in the Spruce-gall Aphis (*Chermes*), in plant-lice (*Aphis*), and in many bees, wasps, &c. Also, in the Silk-worm Moth and in *Solenobia*, larvæ arise from unfertilized eggs and these pupæ give rise only to females. This is of interest in that from the unfertilized oogonia of *Chara crinita* only individuals with oogonia arise.

Cases similar to *Chara crinita* are thought to exist in several plants found in water or on moist substratums. In the genus *Syzygites* (now included in *Sporodinia*), a mould-like Fungus belonging to the Mucorini (*cf.* p. 54), the protoplasm in the conjugating branches forms the starting-point of new individuals without any actual fusion or conjugation taking place. So also in the Saprolegniaceæ it often happens that the egg-cells in the oogonia form new plants without being fertilized; probably renewed investigations will bring to light similar relations in many Peronosporeæ, Siphonaceæ, &c.

Amongst the Mosses parthenogenesis does not seem to be so very rare. In them, as in Characeæ, fertilization is accomplished by means of water; the plants are wetted by rain and dew, and this moisture is held by capillarity in the chinks, &c., between the leaves. The fertilizing spermatozoids travel some distance, swimming through the water to reach the archegonia. This distance is not very great in many forms, and these ripen their fruits freely. But there are several species in which only male plants occur in one locality and female plants in another—it may be hundreds of miles away. Such species are *Paludella squarrosa*, which occurs in North Tyrol with antheridia, and in Bohemia with archegonia only; *Grimmia Hartmanni*, found in the Alps with antheridia, and in the Carpathians with archegonia. *Neckera Besseri*, *Aulacomnion turgidum*, *Bryum alpinum* and *B. Duvalii*, *Didymodon ruber*, *Barbula recurvifolia*, *Amphoridium Mougeotii*, *Mnium insigne*, *Pterogonium gracile*, *Hypnum rugosum*, and *Thuidium abietinum* are further examples of which we cannot treat here in detail. As it is impossible for the archegonium of a Moss in the Carpathians to be fertilized by a spermatozoid from an antheridial plant in the Alps, and as fruits are ripened nevertheless, though not very abundantly in truth, it may well be that these are

cases of parthenogenesis, cases, that is, of egg-cells which continue their development unfertilized.

Amongst Flowering Plants, also, cases are known in which ovules sometimes, without ever being fertilized, form embryos which grow up into healthy plants. An instructive example is the case of *Gnaphalium alpinum* (=*Antennaria alpina*), a perennial Composite nearly allied to both the common Cat's-foot (*Gnaphalium dioicum*) and *Gnaphalium carpaticum* of the Alps and Carpathians. This plant occurs in Scandinavia from Telemarken to Havosund (59° 52′ to 71° north. lat.), and in Russia from Finland to the Kola Peninsula, also in Arctic Siberia, in Arctic America, in Labrador, Melville Peninsula and the whole Arctic Archipelago, in Greenland between the parallels 60° and 72° north lat., finally in Iceland. Thus it is distributed in a zone surrounding the North Pole, some 12° in breadth. It is absent from the mountains of Central and Southern Europe, and is not known to exist, for certain, on the mountains of Central Asia. In these northern latitudes *Gnaphalium alpinum* is exceedingly common, occurring abundantly in innumerable localities. But it is a remarkable fact that neither in Arctic America nor in Arctic Asia has a plant producing pollen ever been found. In the Scandinavian Flora once, in the year 1842, a pollen-bearing plant was alleged to have been discovered; but this has been discredited. A large number of Botanists, thoroughly familiar with the Scandinavian Flora, are unanimous in saying that they have never seen stamen-bearing flowers, and that ovaries only occur. I have myself obtained plants of *Gnaphalium alpinum* from the Dovrefjeld in Norway, and have flowered them in my garden. Every flower produced an ovary but no pollen, so that the possibility of pollination was excluded. A number of achenes ripened containing good seeds, and these, carefully cultivated, produced plants, in all respects similar to the parent form. When these young plants flowered the same phenomena occurred. Thus, one has good grounds for asserting that *Gnaphalium alpinum*, throughout the wide area of its distribution, is propagated parthenogenetically, and that its reproduction is not hindered by the absence of pollen-bearing plants.

Another plant, of which it has been long known that embryos arise in its unfertilized ovules, is a species of Dog's Mercury (*Mercurialis annua*, see fig. 345), one of the Euphorbiaceæ, widely distributed in fields and gardens, in hedge-backs and waste places, throughout Central Europe. Some individuals of this species produce staminal flowers only (fig. 345 [1]), others, female flowers only (fig. 345 [2]). Its dust-like pollen is conveyed to the stigmas by currents of air, and the ovaries of the female flowers ripen seeds freely as the outcome of fertilization. But female plants have often been cultivated in pots by themselves, with the result that they also ripened seed, though smaller in amount than when there is access to pollen, as is the case with plants growing freely in the open. These results were much canvassed, and discredit thrown upon them by many. It was urged that the dust-like pollen might have come from afar, in the air, and have entered the conservatory in which the experiments were conducted; and again it was

pointed out that many female plants of *Mercurialis annua* bear here and there a male flower alongside the female ones. For the refutation of these objections fresh experiments were necessary in which every precaution should be exercised to eliminate sources of error. Such experiments should be conducted in some district in which for miles around the plant did not grow wild, so that the possibility of casual introduction of pollen might be excluded. Fulfilling this requirement is the Central Tyrol, from which both the annual and perennial species of Dog's Mercury are absent. Accordingly I repeated in my upland garden in the Tyrolese Gschnitzthal the cultural experiments originally carried out in 1833 by Ramisch at Prague. Every precaution was taken to avoid sources of error;

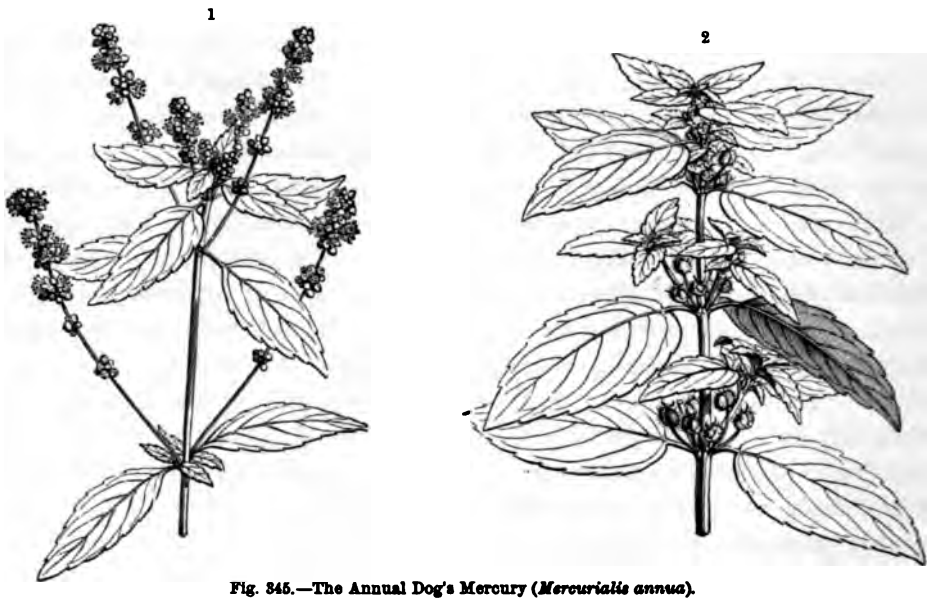

Fig. 345.—The Annual Dog's Mercury (*Mercurialis annua*).

[1] With male flowers. [2] With female flowers.

and in particular were all plants destroyed which showed a tendency to produce male flowers, and the utmost vigilance kept lest an isolated male or hermaphrodite flower should make its appearance anywhere. At the time when the stigmas were ready to be pollinated there were no pollen-grains of this plant anywhere in the neighbourhood for miles around, so that the possibility of such a pollination was excluded. Nevertheless the ovaries set and fruit was ripened, and from the seeds young plants arose.

Another plant, also belonging to the Euphorbiaceæ, in which embryos arise in unfertilized ovules, is *Cœlebogyne ilicifolia*. It was introduced into Europe from the bush of Eastern Australia in 1829, and is now in general cultivation as a hot-house plant in Botanic Gardens. The first specimen introduced bore only female flowers, and all the plants which have been raised from this specimen, and distributed over Europe, resemble it in this respect. Plants of *Cœlebogyne* with male flowers are unknown in European conservatories. The possibility of such

occurring on the female plants (*cf.* p. 300) has not been ignored, but they have never been detected on the plants used for observations; consequently its own pollen has never had access to the stigmas of the plants in question. In spite of this, ripe seed has been obtained and new plants raised from it, which, in their turn, bore only female flowers. Nor do these new plants differ in any way from the plant originally introduced; this observation is of importance, as it might be suggested that they were hybrids, that the pollen of some other euphorbiaceous plant had reached the stigma, there produced pollen-tubes and fertilized the ovules of *Cœlebogyne*. But this is not so, otherwise the offspring would give some indication of such origin. And the plant itself gives indication that it is not fertilized by any pollen. If a plant of *Cœlebogyne* be kept apart where no pollen has access to it, it can be noticed that its stigmatic lobes remain quite fresh for a long time, even till the ovary begins to swell. Only later do they fade, when the seeds are well advanced. This observation is of value since in ordinary cases the stigmas fade very soon after pollination, and it is only unpollinated stigmas which retain their freshness (*cf.* p. 285). In view of these oft-confirmed results, from which all possible source of error has been eliminated, we may conclude that the ovules of *Cœlebogyne ilicifolia* are able to produce embryos without the co-operation of the male protoplasm.

We may now consider whether the instances just described can be regarded as cases of true fruit-formation. As the essence of fruit-formation is a union of ooplasm and spermatoplasm, or in other words, fruit-production must be preceded by fertilization, and as this condition is not fulfilled, these structures are not true fruits. In the absence of fertilization, we must regard these reproductive bodies as brood-bodies, or a special form of offshoot. As has been previously mentioned (p. 44), brood-bodies can arise from any portion of a thallus, from any portion of the stem, and from leaves of the most various kind. A brood-body can originate from the protoplast of a cell of a Lichen-thallus or of a Moss-leaf, from one in the root of an Ash-tree or in the stem of an Orange Lily, on the margin of an Orchid-leaf, or over the midrib of a Begonia-leaf; why not also from the protoplast in the oogonium of *Chara crinita*, or in the archegonium of a Moss, and in the ovules of *Gnaphalium alpinum*, *Mercurialis annua*, and *Cœlebogyne ilicifolia*? Experience shows that in the great majority of cases, both in the Cryptogams and in the Phanerogams, the young commencements of the fruits abort if the ooplasm be denied the spermatoplasm which should fertilize it; but it also shows in unmistakable manner that in a few plants the ooplasm does not die even in the absence of fertilization.

Without entering upon profitless speculations belonging to the domain of Nature-philosophy, we may discuss the question of the possible reasons for the curious behaviour of the "fruits" in these cases. And first of all it may be observed that all the plants exhibiting the phenomenon of parthenogenesis are dicecious. For such plants a crossing with other individuals is alone possible. But what occurs should a crossing in such plants be impeded from any cause? It

seems contrary to the economy of plants that the egg-cell, produced at great expense of energy, and in a sense the culmination of a plant's activity, should wither away unproductive. Plants with hermaphrodite flowers can, if denied crossing, resort to autogamy. But this is of course impossible with dicœcious plants; instead of autogamy the formation of embryos in unfertilized oogonia and ovules is a possibility open to them, whereby their outlay of material and energy shall not be wasted. Dicœcious plants, which are likewise annuals, are especially liable to the danger of extinction in the absence of pollen and consequent fruit-production; for them the death of the individual may connote the disappearance of the species. Against such possibilities many precautions exist amongst plants, notably the formation of offshoots or brood-bodies; the leafy shoots arising from these structures preserve the plant from such a contingency. In the same way we may regard the formation of brood-bodies in the ovules of dicœcious plants as a means contrived to prevent the extinction of the species. The fact that brood-bodies are formed in the ovules of not a few dicœcious plants to which pollen has not ready access, supports this view. There has been a specimen of the Californian bush, *Obione halimifolia* (an *Atriplex*, Chenopodiaceæ), for many years in the Vienna Botanic Garden. This plant is dicœcious; the Vienna plant bears only female flowers, and pollen is not accessible within hundreds of miles. Its stigmas remain unpollinated, and its ovules unfertilized. But as the autumn draws in, the ovaries of this plant begin to swell, and the perianth which ensheaths the ovary expands, and what appear to be fruits are formed. But these fruits are what we call "deaf"; no signs of an embryo are to be found within. Thus, in this plant, no brood-body has been produced; it is impossible to say whether or no, at some former period, this plant ripened brood-bodies in its unfertilized ovules. Why the male plants of *Chara crinita* are absent from the Baltic, and those of *Gnaphalium alpinum* from the Arctic regions, are puzzles as yet unanswered. In *Chara crinita* it is only on the coast-regions that male plants are wanting; inland, male and female plants grow side by side. Possibly, climatic conditions and the vicissitudes to which our existing Flora has formerly been subject have brought this about, but we lack the data for continuing the discussion further.

If, in the plants enumerated, parthenogenesis be but a special case of offshoot formation, it is a matter of indifference which cells within the ovule are the starting-points for the brood-bodies. In *Cœlebogyne*, in addition to the egg-cell, other cells belonging to the wall of the embryo-sac are concerned in the production of brood-bodies. Cells quite outside the embryo-sac can also initiate these offshoots; in which case they project as little papillæ into the cavity of the embryo-sac, where they continue their development. In this way several embryos may arise side by side, a condition which has been termed *Polyembryony*. This phenomenon occasionally takes place in the ovules of hermaphrodite flowers, in which a normal pollination and passage of pollen-tubes to the micropyle occur. This is the case in certain Liliaceæ, polyembryony having been observed in species of

Funkia and *Allium*, in both of which normal fertilization takes place. It is interesting to note that in the case of *Allium odorum* recent investigations show that the accessory embryos arise actually from the *antipodal cells* (*cf.* pp. 416, 417), *i.e.* from cells at the base of the embryo-sac which, in ordinary cases, simply atrophy. Usually one embryo only arises from this source, but occasionally all three antipodal cells develop into embryos. The ultimate fate of the embryo arising (by fertilization) from the egg-cell and of those arising from the antipodal cells has not been ascertained.

A peculiarity of parthenogenesis consists in the fact that the brood-bodies arising in the ovules assume the form of embryos, not distinguishable from embryos resulting from fertilization of an egg-cell. Little tubers or buds produced in the ovary in places of ovules, as in *Amaryllis* and *Crinum* (*cf.* p. 44), partake of the nature of branches of the plant producing them; but the offshoots which arise within ovules are not branches but young plants, provided with root, stem, and leaves, and they are nourished by a special tissue which cannot be interpreted as a portion of the axis of the young plant. These offshoots arising within the ovule possess a new and independent axis, and herein exhibit an essential difference from the offshoots described in the last chapter. Why these offshoots in the ovules always assume the guise of embryos is a problem which we shall not solve, perhaps, until we have more knowledge as to the essential differences in property between the protoplasm of the ovule and that of other plant-organs.

HETEROMORPHISM AND ALTERNATION OF GENERATIONS.

A sight of the sea-anemones and ever-varying polyps and corals, viewed through the blue-green waters of a shallow bay, at first suggests a kaleidoscopic assemblage of blossoming plants. At a distance the crowns of expanded tentacles resemble red and purple Asters or the flowers of Mesembryanthemums; the skeletons of these organisms are not unlike, in their ramification, the branching of some tufted plant. The corals and polyps, like plants, are denied free movement, and like red and other seaweeds, are attached to their stony substratum. Very appropriate then, in view of their characteristic appearance, is the name of Zoophytes which Zoologists gave to these animals.

And in their internal structure and mode of life they present certain remarkable points of resemblance to plants. In many species the single individuals which are joined together into a colony behave quite like the organs of a body, or the members of a single organism which discharge different functions. There is a division of labour amongst the individuals or polyps of the colony. One branch of the colony is concerned in the acquiring of nutrition, another in reproduction, yet they have a common digestive cavity, so that the juices obtained by one portion may be shared by others which cannot take them up from the environment for themselves. To this differentiation amongst equivalent members we may apply the term *Hetero-*

morphism; it will be seen in the sequel that Heteromorphism is a condition of wide occurrence amongst plants.

Zoophytes propagate themselves in two ways. They may produce buds which grow into new individuals, just as buds arise on the branches of a tree and grow into new branches; and, like the latter, the products of these buds remain attached to the part of the colony producing them, so that ultimately the extent of the colony is considerably augmented. In many Zoophytes, especially in the Polypomedusæ, certain branches of the non-sexual polyp-form assume the form of cups or capsule-like structures in which buds arise which grow into disc-like, free-swimming medusæ, with a crown of tentacles. These medusæ contain sexual organs, and from each of their fertilized eggs an embryo arises which becomes attached to the sea-bottom, and grows either into a non-sexual polyp or into a group of sexual medusæ. In the last-named event the pear-shaped embryo, after swimming about for a while, becomes attached by its pointed end. On its body arise a number of ring-like furrows, which gradually deepen until the cone-shaped embryo is segmented into a number of transverse discs. Ultimately the cone disarticulates and the discs swim away as medusæ. These medusæ are sexual persons, and from the fertilized egg-cells, either sexual or non-sexual generations may arise. This alternation of sexual and non-sexual persons is known as *Alternation of Generations*.

Thus within the limits of the Zoophytes we see displayed two entirely distinct things. First, heteromorphism, which gives us equivalent polyps on the same colony, variously modified for the discharge of different functions; secondly, alternation of generations, in which medusa-forms (sexual persons) arise by a process of budding from polyp-forms (asexual persons), and give rise, by a sexual process, to fresh polyps. Alternation of generations is an alternation of sexual and asexual individuals, the one giving rise to the other.

Both these phenomena are widely manifested amongst plants. The plant-body amongst the Flowering Plants may be regarded as an assemblage of shoots. Each shoot or branch-system consists of a series of members, of which the upper and younger ones are developed with the assistance and co-operation of the lower and older. These shoots are all united together, and the tissue which unites them, with its conducting-tubes and air-lacunæ, may be regarded as an organ common to them all. From the fact that the several shoot-members have the capacity of independent existence, when separated from one another, they have been regarded as individuals and termed "Anaphytes" (*cf.* p. 6). Shoots, united together into a plant-body, possess a common household, and division of labour is manifest amongst them. The Anaphytes of the foliage region serve especially for the preparation of food-stuffs, those of the flowering region for the production of sexual cells and fruits. Shoots of the latter kind are termed flowers, of the former foliage-shoots. Shoots arise from buds, and these may be similarly distinguished into flower-buds and foliage-buds. Those which arise from foliage-buds remain, for the most part, attached to the plant-body, appearing as branches of the same; those, on the other hand, which arise from flower-buds ultimately disarticulate,

leaving a scar. Thus we see the shoots of a plant-body are variously modified, and we may speak of a *heteromorphism* in this connection analogous to that existing amongst the polyps of a coral.

It not infrequently happens, amongst purely foliage-shoots, that the lateral shoots (or anaphytes) bear foliage quite unlike that borne by the shoot that gives them origin. In many perennial shrubs and trees a long series of asexual shoots arises, of which the lowest and highest are so different, that one might easily suppose them to belong to different species of plants; or that a gardener had grafted a bud of another species upon the plant. The shoots of young Ivy plants (*Hedera Helix*), whether creeping on the soil of the forest-floor, or climbing up the trunks of trees or steep rock-faces, bear shortly-lobed, white-veined, dull-looking leaves, and produce a large number of attachment-roots which hold the shoot to the substratum. The shoots of an old plant, however, developed high up on the tree crown, or over the top of the wall, bear bright shining, heart-shaped leaves without conspicuous veins, nor do they produce roots at all. It is this latter class of shoots alone which bring forth flowers; the creeping shoots never do so (*cf.* vol. i. p. 709).

This contrast between the appearance of the shoots of a young plant and those produced in later years is much more marked in the Aspen (*Populus tremula*). The foliage-leaves of the first year's shoots are triangular, cordate at the base, and only shortly stalked, they are also hairy on the under surface; those arising on the shoots of a thirty-year-old Aspen are circular in outline, smooth on both sides, and provided with long petioles. Similar is the case of many Willows, Oaks, and Myrtaceæ; in the last-named family the Australian *Eucalyptus globulus* is worthy of mention. The leaves on its first year's shoot are sessile and cordate at the base, whilst on the grown tree they are stalked and curved like a boomerang. Very marked, again, are the differences in the character of the foliage-leaves on the successive shoots of the Junipers (e.g. *Juniperus excelsa, japonica, phœnicea, chinensis*, and *Sabina*). The leaves on the younger branches (for the first ten years about) are acicular, stiff and spreading; those on the shoots of later years are short, scale-like, and closely imbricating. Worthy of note in this connection is the contrast of long and short branches seen in many Conifers, *e.g.* the Larch (*Larix*). Though the actual leaves are not dissimilar, their insertion is, and the length of the shoots producing them. Whilst the short branches do not attain a greater length than 1 centimetre, the long branches reach to 15 or 25 cm.; to this contrast is due in large degree the altogether peculiar physiognomy of the Larch-tree, as shown in fig. 354 (*cf.* also, fig. 337 [1], p. 443).

The fruit-trees in our orchards are some years covered with blossom, and, with a propitious summer, they are weighed down with fruit in the autumn. Such "bumper" years are generally followed by a series of lean years, in which little fruit is ripened, or flowers are hardly produced at all. The same thing is observed in forest trees. There is a saying that Firs and Larches only form their cones in plenty once in seven years. This is so far right in that a good

fruiting year is followed, in these trees, by several sparing ones; so much so that it suggests that the trees are exhausted by the heavy production and require time in which to recover, and, by the formation of non-flowering shoots with green foliage, to manufacture and lay by stores of food-material. So also in

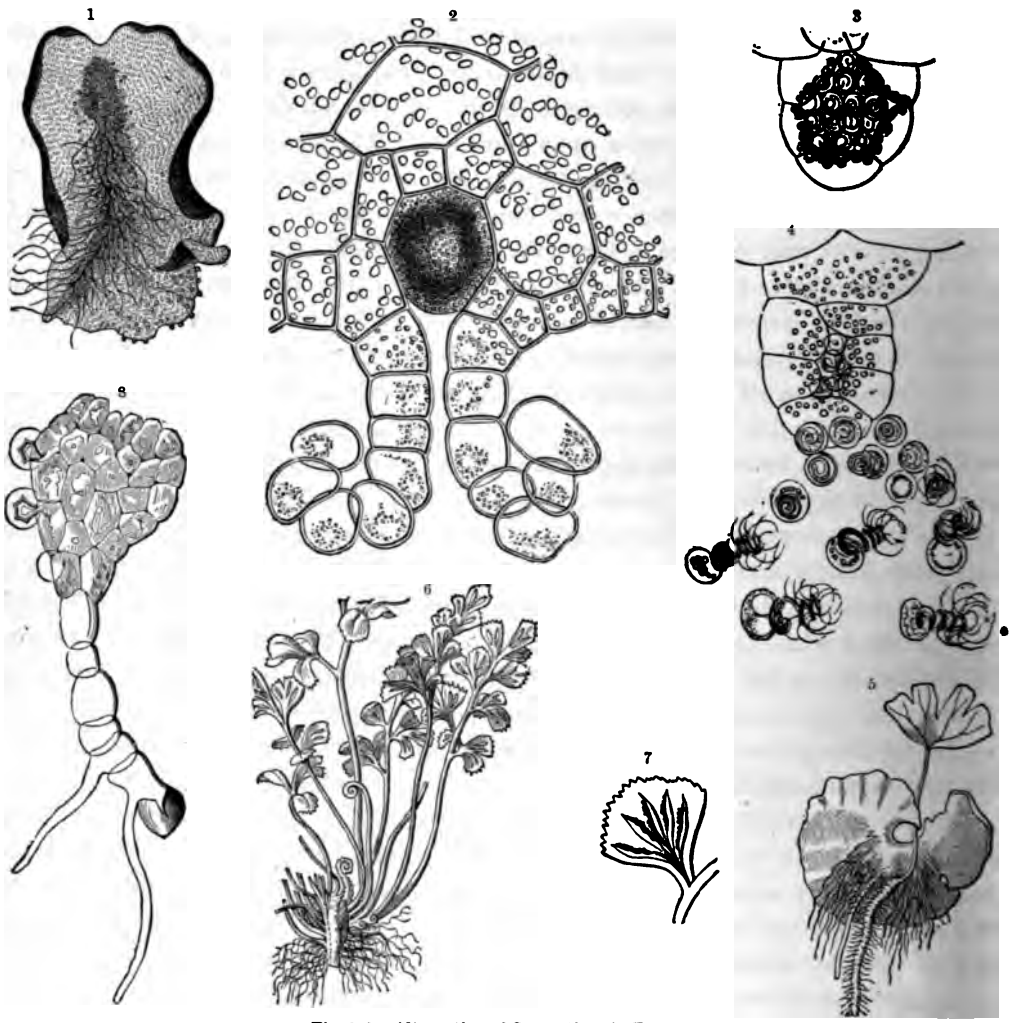

Fig. 346.—Alternation of Generations in Ferns.

[1] A Fern-prothallium seen from the under side; archegonia are present amongst the rhizoids and towards the sinus at the top, antheridia on the margin below. [2] Longitudinal section of an archegonium showing the egg-cell (shaded) in its ventral portion. The canal leading to the egg occupies the neck-portion. [3] Longitudinal section of an antheridium showing the spermatozoids coiled up within. [4] Antheridium discharging its spermatozoids. [5] Commencement of the asexual generation. The first simple frond of the young fern-plant (sporophyte) is held aloft, whilst a root descends into the ground. The young fern-plant is still attached to the prothallium. [6] Complete sporophyte of the Wall-rue Spleenwort (*Asplenium Ruta-muraria*) with its fronds showing sori. [7] Under surface of a pinnule of the sporophyte of the Wall-rue Spleenwort (*Asplenium Ruta-muraria*) showing the linear aggregations of sporangia (sori), with lateral indusia. [8] A young prothallium arising from a spore; the spore is below. [6] natural size; [1] × 8; [2, 3,] and [4] × 350; [5] × 6; [7] × 3; [8] × 240.

many low herbs. Now and then the Orchids in the meadows flower in immense profusion, and we say it is a good "Orchid year"; then follow years in which, in the same localities, hardly an orchid-flower is to be found.

Fig. 347.—Tree-ferns (*Alsophila*) in Ceylon (drawn from nature by Ransonnet).

The impulse to the production of flowering-shoots cannot entirely depend on the prevailing climatic conditions of the year in which the flowering takes place. For in the autumn of the previous year the bud is already laid down, and one can tell by dissecting it whether it will form a flowering or a foliage-shoot. In associating climatic conditions with flower-production, it is the summer of the year previous to flowering which must be taken into account. This is well illustrated by the seasons of the years 1893 and 1894. The summer of 1893 was, as is well known, remarkable for its warmth and long-continued sunshine. This was followed in 1894 (to take an example to hand) by the flowering of many plants in Kew Gardens which are hardly ever known to flower there in the open, under ordinary circumstances. Of these it will be sufficient to mention two Gymnosperms, *Ephedra* and the Maidenhair tree (*Ginkgo biloba*).

Fig. 348.—*Rhipidopteris peltata* showing sterile fronds to the left, and fertile ones to the right.

It is easy to observe the fact that in a big tree, of which one side is in the full sun whilst the other is shaded, the shady side produces foliage-shoots for the most part, whilst the sunny side blossoms freely. Nor can one resist the conclusion that it is the sunshine which stimulates the flowering. The same thing is shown by plants, which, growing in dense forest shade, remain without flowers from year to year: but as soon as the trees about them are felled, and the light gains entrance, form flower-buds, and ultimately blossoms and fruits. The advantages accruing to the plant by this change in its surroundings have already been indicated on pp. 394 and 459; but what immediate influence the sunlight has on the building capacity of the plant, and how it is that the tissue which, in the shade forms a foliage-bud should in the sunshine form a flowering shoot, must for the present remain unanswered.

And now, as regards *Alternation of Generations*. The relations between the sexual and asexual generations are very various in different portions of the vegetable kingdom. In some groups of plants the two generations are obvious and distinct, in others it is very difficult to draw the line between them. In the Ferns, Horsetails, and Vascular Cryptogams generally, the two generations are quite distinct and easily recognizable. In the Ferns the generation which bears the sexual organs (=sexual generation or oophyte) takes the form of a small, expanded plate of cells, from the under side of which delicate hair-like rhizoids are developed which penetrate the soil (see fig. 189[16], p. 11, and fig. 346[1]). This plate-like structure is usually known as the *prothallium*; it is either heart-shaped or ribbon-like and lobed, attaining a length of from ·5 to 1 centimetre. The sexual organs

are borne on the under surface of the prothallium; the antheridia as little hair-like structures distributed over the surface (fig. 346 [3]), the archegonia, flask-like in form, and having the expanded ventral portion sunk in the substance of the prothallium and the neck projecting (see fig. 346 [2]). In the majority of Ferns both sorts of sexual organ occur on the same prothallium, the archegonia on the central parts and in the region of the notch or sinus, the antheridia towards the margin and on the lobes. Fertilization is brought about by the escape of spirally twisted

Fig. 349.—*Platycerium alcicorne* (drawn from nature by Selleny).

spermatozoids from the antheridia (fig. 346 [4]), which enter the neck of the archegonium, one of them fusing with the egg-cell contained in the ventral portion of that organ (fig. 346 [2]). We may regard the fertilized archegonium as the fruit. It does not become detached from the prothallium, but the fertilized egg-cell develops *in situ* into the next (or asexual) generation, which differs altogether from the sexual one. The egg-cell divides into several cells, one of which gives rise to the young stem, another to the first frond, a third to the primary root, whilst a fourth forms a sucker or "foot", which maintains communication for some time with the tissues of the prothallium (*cf.* fig. 346 [5]). Soon after the first simple frond is expanded, a second is formed, and the young fern-plant is now able to continue its development independent of the prothallium. The prothallium now dies away, and in its place

we have the young fern-plant with its fronds (*cf.* fig. 346 [6]). The fern-plant bears no sexual organs, and must be regarded as the asexual generation (or sporophyte). Its first fronds provide the necessary food-materials for the production of new fronds, which arise in increasing numbers from the stem-apex; as a rule the stem remains short, or it may be elongated horizontally as a rhizome, or, in the Tree Ferns (*cf.* fig. 347), it develops into an erect caudex bearing a tuft of green fronds at its apex. In addition to their purely assimilating function, the fronds are concerned in the propagation of the plant, and produce quantities of spore-cases (or sporangia) containing spores. These sporangia arise in clusters, known as sori, and are usually situated on the under sides of the fronds (see figs. 346 [6] and 346 [7], and fig. 189, p. 11). In the majority of Ferns these two functions—assimilation and spore-production—are performed by one and the same frond, and there is no especial difference in structure between the assimilating and spore-producing portions. But in the so-called "Flowering Fern", or Royal Fern (*Osmunda regalis*), these two portions of the frond stand out in marked contrast; the topmost pinnules of the frond are entirely covered with sporangia, and light brown in colour, whilst the lower portions are bright green, and quite destitute of sporangia. In the Hard Fern (*Blechnum Spicant*) and Parsley Fern (*Allosorus crispus*) there is a distinction between the sterile and fertile fronds, the pinnules of fronds which bear sporangia being much narrower than those of purely assimilating fronds. In *Rhipidopteris peltata*, again the fertile fronds are disc-like, whilst the assimilating fronds are branched and filamentous (see fig. 348); in *Platycerium alcicorne* the fertile fronds are branched like a reindeer horn, whilst the sterile ones form great green discs in close contact with the bark of the tree on which it grows, and remind one of huge prothallia (see fig. 349). As soon as the spores are mature they are discharged from the sporangia and scattered by the wind. Falling on moist earth, on the bark of a tree, or in a rocky cleft, they germinate, producing prothallia, upon which the sexual organs are borne (*cf.* fig. 346 [8]). Thus in the Fern, two stages are well shown in the life-cycle, (1) the prothallium, the sexual generation or oophyte, and (2) the fern-plant, the asexual generation (or sporophyte), which bears spores, these in turn give rise to the first generation again.

In the Horsetails (Equisetaceæ), which have been figured and referred to at p. 14, a similar alternation of generations occurs. The fern itself is the asexual generation, and bears cones of sporangium-producing scales. From the contained spores prothallia are formed. In several species of Horsetail (e.g. *Equisetum sylvaticum*, fig. 190 [7], p. 14) one and the same shoot bears the organs of assimilation and spore-production; whilst in other species (e.g. *Equisetum arvense*) these functions are relegated to distinct shoots; *i.e.* shoots formed in spring, which terminate in cones (fig. 190 [2], p. 14), and others formed later, which bear numerous green assimilating branches, but no cones (fig. 190 [1], p. 14).

In the group of the Lycopodinæ very interesting conditions prevail. In the so-called Club Mosses (Lycopodiaceæ) the plant is much branched, and in a great many species of *Lycopodium* (e.g. *Lycopodium annotinum*, fig. 378) the shoots end

in cones of closely-fitting scales, each of which bears a sporangium. The spores in *Lycopodium* are all alike, and on germination form prothallia, which bear antheridia and archegonia. It is interesting to note in passing that we have only become acquainted with these prothallia in recent years, and for the most part in exotic species. The prothallia of a limited number of European species, however, have been seen. Included in the Lycopodinæ is the genus *Selaginella* (*cf.* fig. 111[1], vol. i. p. 421), resembling *Lycopodium* in its moss-like habit, but differing from it in that *two sorts of spores* are produced. These spores, known as *macrospores* and

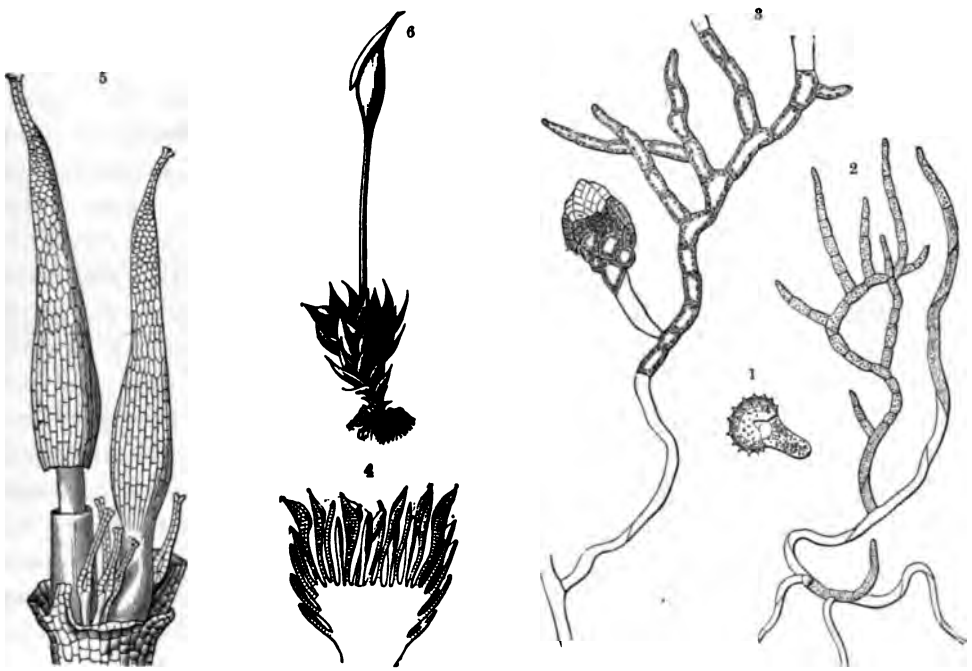

Fig. 350.—Alternation of Generations in Mosses.

[1] A spore germinating. [2] A moss-protonema. [3] Protonema giving rise to a bud from which will arise a leafy moss-shoot. [4] Longitudinal section of tip of a male shoot of a moss-plant; antheridia are present between the scales. [5] Tip of a female shoot with archegonia; two of them have much enlarged due to the swelling of the young sporogoniums within. [6] Leafy female shoot of a moss-plant with fully developed sporogonium at its tip. Spores arise asexually in the terminal capsule. 1, 2, 3 × 350–400; [4] × 15; [5] × 80; [6] × 5.

microspores, arise in different sporangia in the same cone, in many cases. The macrospores are relatively large, and are contained four in a sporangium; the microspores are small, and a large number of them is present in a sporangium. The prothallia resulting from their germination are of two kinds; the macrospore gives rise to a female prothallium which bears archegonia; the microspore to a much reduced male prothallium bearing a single antheridium. The sexual generation—which in the Fern consists of *one structure*, the prothallium—here consists of *two structures*, the male and female prothallia. After fertilization the archegonium gives rise to a new, asexual *Selaginella* plant.

This differentiation amongst the spores in *Selaginella* (in consequence of which the plant is termed *heterosporous*, in contradistinction to Ferns, and *Lycopodium*,

which, having one sort of spore only, are termed *homosporous*) is of interest, since it leads on to the condition prevailing in Flowering Plants. In these the alternation of generations is not obvious, no recognizable and detached sexual generations being seen. But on certain shoots of flowering plants (*i.e.* in the flowers) sporangium-bearing leaves are borne; these are the stamens and carpels respectively. The sporangium borne by the stamen is the pollen-sac, and the contained pollen-grains are the microspores. The microspore or pollen-grain, when it germinates on the stigma (or in the micropyle, in Conifers, *cf.* p. 418) forms a pollen-tube, which contains the male fertilizing element, corresponding to a spermatozoid. Of course the conditions of fertilization in most Flowering Plants are altogether different from those obtaining in the Vascular Cryptogams, and motile swimming spermatozoids are very rarely produced. The sporangium borne by the carpel, on the other hand, is the ovule, and the embryo-sac contained within the ovule is regarded as the macrospore. As a rule but one macrospore is met with, but in certain Amentaceæ (e.g. *Carpinus*, see fig. 314A, p. 412) more embryo-sacs (macrospores) than one are present. In the Flowering Plant the macrospore is not shed from its sporangium (ovule), but germinates *in situ*, forming an egg-apparatus (*cf.* fig. 316 and p. 417), and certain other cells, which ultimately form the endosperm. These structures are regarded respectively as corresponding to the archegonium and female prothallium of such a heterosporous Vascular Cryptogam as *Selaginella*. If the contents of the embryo-sac in Gymnosperms (see p. 415) and in Angiosperms (see p. 417), respectively, are compared with the female prothallium of *Selaginella* or other heterosporous Vascular Cryptogam, it will be seen that the Gymnosperm shows the greater agreement. In it the archegonia are still quite recognizable as such, though these now take part in quite a different type of fertilization. In all Flowering Plants (Gymnosperms and Angiosperms) as opposed to the Vascular Cryptogams, the microspores produce pollen-tubes in the vicinity of the ovules, and these penetrate to the embryo-sac (macrospore) and fertilize the egg-cell. In the case of *Ginkgo* and the Cycads, however, these tubes liberate motile spermatozoids before the archegonium is reached, so that a vestige of the Cryptogamic method is still retained.

Thus we see that in Flowering Plants the female prothallium or sexual generation is hidden away in the embryo-sac, and is never an independent structure. This fact is correlated with the different manner of fertilization which obtains in Flowering Plants as compared with Vascular Cryptogams.

In the Mosses the sexual organs are formed at the tips of little leafy shoots; fertilization is much as in Ferns, and from the fertilized egg a new (asexual) generation arises. This generation, known in Mosses as the sporogonium, consists of a stalk (the seta) terminating in a spore-capsule above. The sporogonium develops within the archegonium on the sexual generation of the Moss. The base of the seta penetrates some distance into the fertile Moss-shoot, and is in this way able to absorb nourishment. As the sporogonium elongates, the archegonial wall stretches with it up to a certain point, then it breaks across transversely and the upper portion is raised up on the capsule as a sort of hood or extinguisher (the

calyptra, see figs. 350[5] and 350[6]). Ultimately this hood is thrown off and the capsule, within which quantities of spores are produced, opens. The spores are readily distributed by the wind shaking the capsule on its stalk. It should be noted that in Mosses this asexual generation (the sporogonium) never becomes independent of the sexual Moss-plant; the base of its stalk always remains embedded in the tissues of the sexual generation. In the Ferns, on the other hand, the

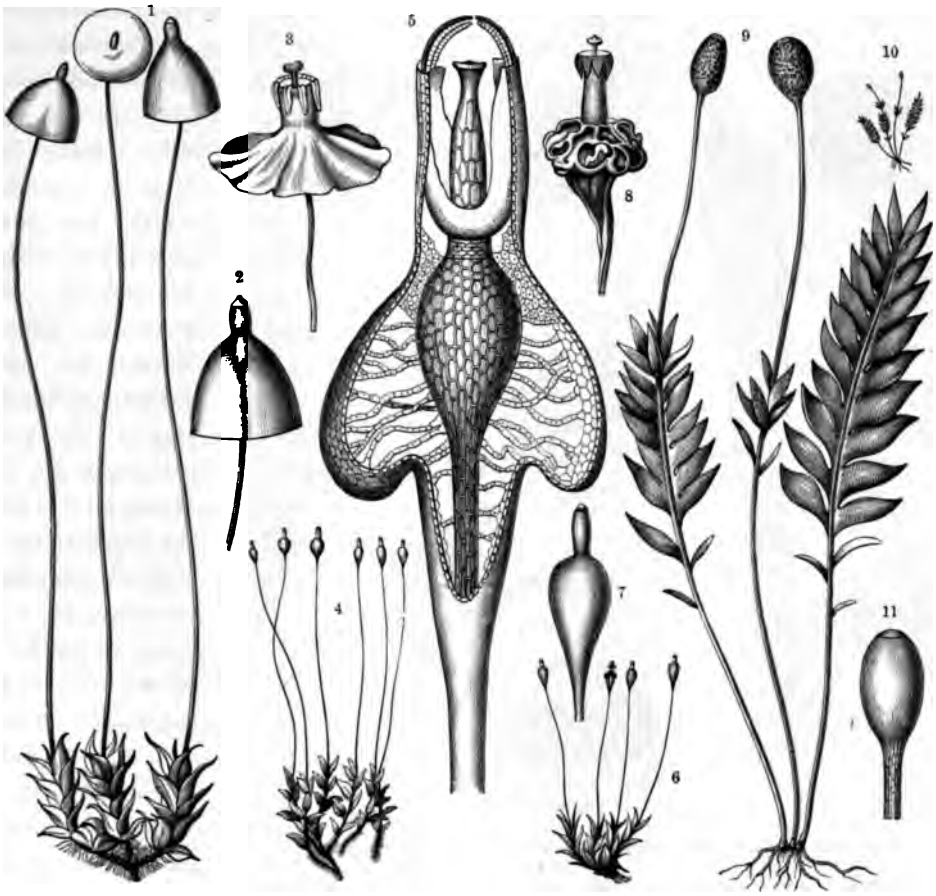

Fig. 351.—Alternation of Generations in Mosses. Various forms of sporogonium, which as the asexual generation have been produced at the tips of leafy shoots.

[1] *Splachnum luteum*. [2] An unripe capsule of the same. [3] A ripe and open capsule of the same. [4] *Splachnum vasculosum*. [5] Longitudinal section of a ripe capsule of this Moss. [6] *Splachnum ampullaceum*. [7] An unripe capsule. [8] A ripe capsule of the same. [9] and [10] *Schistostega osmundacea*. [11] A ripe capsule of the same. [1], [4], [6], [10] natural size · [2], [3] × 2; [7], [8], [9] × 10; [11] × 15; [5] × 100.

asexual generation (=the Fern-plant), though at first drawing nutriment from the prothallium (*cf.* p. 475) by its "foot", soon becomes quite independent, the prothallium dying away. The form of the sporogonium is very varied in different groups of Mosses. In fig. 351 are shown the sporogonia of a number of Mosses, including species of *Splachnum* (*S. luteum*, *S. vasculosum*, and *S. ampullaceum*), a rare form occurring on the excrements of cattle, reindeer, &c., that of the already-mentioned Luminous Moss (*Schistostega osmundacea*, *cf.* vol. i. p. 385); and in fig. 191, p. 16

those of *Polytrichum, Bryum, Hylocomium, Andreæa,* and *Sphagnum.* The spores of the asexual generation germinate on a moist substratum, giving rise to a tubular filament which becomes segmented, and gives rise to a considerable growth of simple character, known as the *protonema* (see fig. 350 [2]). Certain rows of cells of the protonema are colourless and penetrate the ground as rhizoids, the others are extended on the soil and are bright green in colour. After a while bud-like structures arise here and there upon the protonema (see fig. 350 [3]); these develop into leafy Moss-shoots, upon which the sexual organs are borne—usually in little clusters. Thus in Mosses, the sexual generation has two stages; the protonema and the leafy Moss-plant. From the latter arises the asexual generation or sporogonium. In many of the Liverworts the sexual generation is much simpler, consisting of a thallus, in which the archegonia and antheridia are sunk. However, a great variety is met with amongst them, but the main relations of the sexual and asexual generations are much as in Mosses.

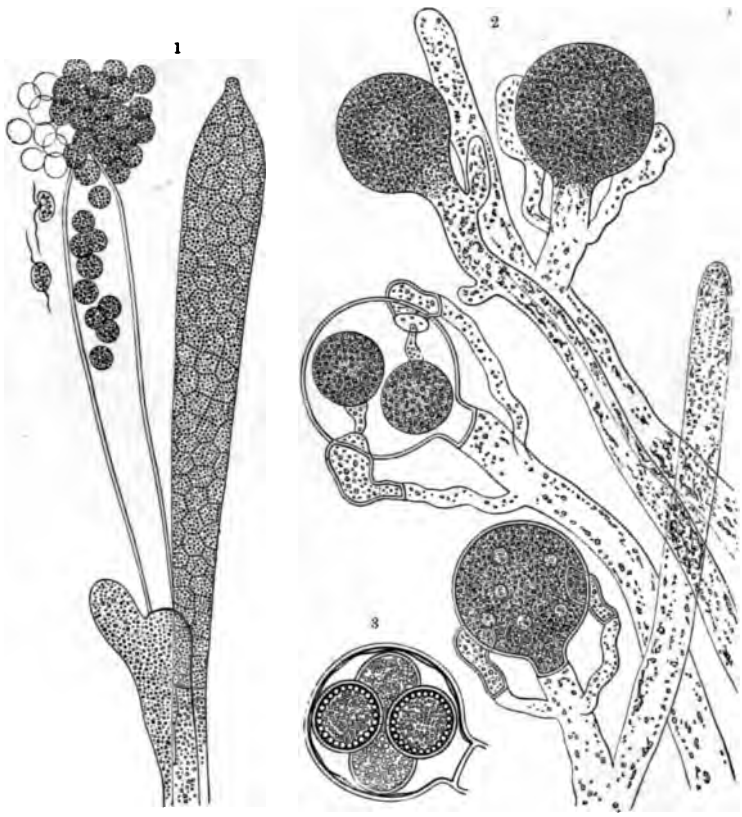

Fig. 352.—Asexual and sexual reproduction in Saprolegniaceæ.

[1] Formation of asexual zoospores in *Achlya.* [2] Oogonia with antheridia and fertilizing tubes. [3] Fruit. All figures × 300. (After Sachs.)

It will be noted that in Mosses the sexual generation is much more complex a structure than the corresponding structure (the prothallium) in Ferns. The asexual generation, on the other hand, in Mosses is never independent, whilst in Ferns it becomes so quite soon and attains, in the latter group, to much greater structural complexity than in the Mosses.

Amongst the large assemblage of simple plants which together constitute the class Thallophyta we find in some forms an incipient alternation of generations on the lines already described for Mosses, Ferns, &c.; in others there is no suggestion of

such alternation; and in others again (such forms are numerous), an alternation occurs, but of a character quite different from that of higher plants.

First we will mention such as show an alternation of generations not unlike that of the Fern. It will be remembered that in the Fern there is a simple prothallium upon which the sexual organs arise, and from the fertilized egg-cell a new generation, of considerable dimensions, is developed which produces asexual spores, these in turn giving rise to prothallia. In the group of the Red Seaweeds or Florideæ (*cf.* pp. 61, 62, and figs. 204[7] and 204[9], p. 53), the seaweed plant is the sexual generation and bears the rudimentary fruits with trichogynes and the male spermatia. After fertilization, a considerable growth is initiated, which results in a mass of spores being abstricted, these spores being in many cases inclosed in a sort of capsule, which develops concurrently with the spores. This capsular structure with its spores we may interpret as a very simple asexual generation comparable to the sporogonium of a Moss or to a Fern-plant with its spores. Of course this asexual generation is very ill-marked in the Red Seaweed, and it is difficult to quite draw the line between it and the sexual generation of which it forms a continuation. It has this in common with Mosses and Ferns; that from a single process of fertilization a numerous progeny of spores is begotten—spores which on germinating give rise to sexual plants again.

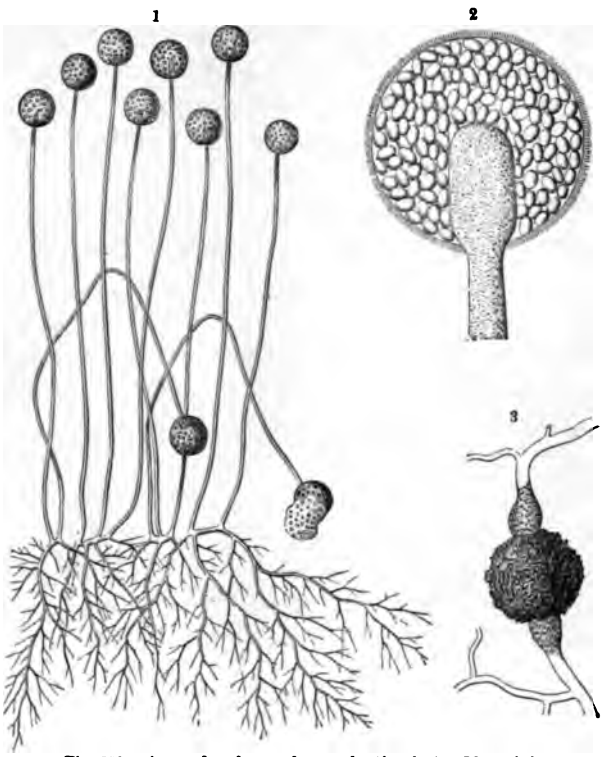

Fig. 353.—Asexual and sexual reproduction in the Mucorini.

[1] Mycelium producing asexual spores in stalked sporangia. [2] A single sporangium in section. [3] Formation of a zygospore. [1] × 40; [2] × 260; [3] × 180.

The brown Wrack, *Fucus*, is an example of a Thallophyte in which alternation of generations is not known to take place. In this seaweed every generation is a sexual generation, and the fertilized egg-cells, so far as is known, give rise—not to spores—but to new sexual generations. Its life-history is described and figured on pp. 51, 52.

And now we come to a type of alternation of generations, prevalent amongst green Algæ and some families of Fungi, which seems to be quite distinct from the rhythmic alternation which obtains in the Mosses, Ferns, &c. The oft-mentioned

tubular Alga, *Vaucheria sessilis* (belonging to the family of the Siphonaceæ) will serve as an admirable example of what we mean. This plant reproduces sexually (*cf.* pp. 57, 58, and figs. 204^5 and 204^6, p. 53) by means of oogonia and antheridia of simple character; it also propagates itself by means of large asexual zoospores which it liberates from the tips of its tubular filaments (*cf.* vol. i. pp. 23, 24, and Plate I., figs. *a–d*). But these two classes of reproduction do not occur simultaneously upon one and the same plant; but rather, so it was till lately supposed, upon generations which alternated with one another either regularly or irregularly. Sometimes the *Vaucheria*-plant arising from a zoospore bore sexual organs, and from the fertilized egg-cell arose a non-sexual plant which gave rise to zoospores again; or a series of asexual generations followed one another, the series being terminated by a sexual generation, the fertilized egg-cells of which entered on a resting stage.

The meaning of this supposed alternation of generations in *Vaucheria* has recently been cleared up by Klebs in a series of very interesting culture-experiments. Without describing these in detail we may briefly indicate some of Klebs's results. If a number of young *Vaucheria*-plants be cultivated, three possibilities are open; the plants may produce sexual organs; they may be reproduced asexually by zoospores; or, finally, they may remain perfectly sterile. Klebs found that by appropriate treatment of plants, he could bring about any of these possibilities at will. Young plants placed in a 2–4 per cent sugar solution, and kept in the light at a temperature not falling below 3° C., invariably produced sexual organs in the course of some ten days. Other plants, which had been grown in a dilute nutrient solution of food-salts in the light for a short time, were removed to water and placed in the dark. These plants soon gave rise to enormous quantities of zoospores; in time these zoospores germinated, and the resulting plants in their turn produced fresh zoospores, and so on. The third condition, that of sterility, was obtained by keeping plants in strong sugar solution (10 per cent), and also by other methods. More than this, the same plants were caused to alter their mode of reproduction by varying the conditions; in this way it was possible to cause them at one time to produce zoospores and at another sexual organs. This brief summary is sufficient to show that a given *Vaucheria*-plant has no inherent tendency to reproduce asexually in preference to sexually, or conversely; and that its manner of reproduction (or its abstention from reproduction) depends on the conditions which prevail outside the plant. Thus, in *Vaucheria*, no true alternation of generations prevails in the sense in which it does in Mosses and Ferns, and every generation is potentially both a sexual and an asexual generation. It is the external conditions which call forth the one or the other.

In a great many other Thallophytes the same is no doubt true, though exact experiments have yet to be performed on the majority of them. We know it to be so in *Botrydium* and in the Water-net (*Hydrodictyon*) and in others. The Water-net (figured on p. 24) propagates asexually by the contents of its cells breaking up into very numerous (7000–20,000) swarm-spores (thallidia) which

Fig. 354.—Larch-trees (*Larix europæa*).

do not forthwith escape, but swim about for a while within the wall of the cell in which they originate. Then they join together into a tiny net which escapes, ultimately growing to its full size (*cf.* vol. i. p. 36). In sexual reproduction a much larger number (30,000–100,000) of small motile bodies (gametes) escape and conjugate in pairs. Klebs has found here also that either of these methods can be produced at will by altering the conditions under which the plant grows.

Among the Fungi the Saprolegniaceæ show well-marked sexual and asexual methods of propagation. These are mould-like forms which attack fish and other aquatic animals upon which they are parasitic. Purely asexual reproduction occurs by means of zoospores which are liberated from long, club-shaped sporangia (fig. 352[1]); whilst sexual reproduction (which may occur upon the same plant) takes place by spherical oogonia arising upon certain branches and antheridia as small lateral twigs below them (fig. 352[2]). The latter perforate the oogonium-wall with their "fertilizing tubes" (*cf.* the allied *Pythium*, p. 56), but curiously enough there is no real fertilization. Nothing has been observed to pass from the fertilizing-tubes to the egg-cells, and we must regard the process of fertilization here as obsolete. The egg-cells, though unfertilized, put on cell-walls (fig. 352[3]) and germinate, as one might say, parthenogenetically.

In the Moulds of the family Mucorini the mycelium establishes itself upon an organic substratum and produces, at one time, long-stalked sporangia (figs. 353[1] and 353[2]), and at another short sac-like outgrowths which arise in pairs near one another and conjugate, forming a zygospore (fig. 353[3]). Whether this or that method of reproduction prevails in these Fungi depends, most probably, on external conditions; indeed examples from amongst the Fungi could be adduced in which careful experiment has determined that this is the case.

In conclusion we may inquire how is it that alternation of generations is so widely distributed amongst plants, whilst in the animal kingdom it is of relatively rare occurrence. We obtain an answer to this question when we consider what are the distinguishing characters of those animals in which alternation of generations takes place. The corals, polyps, and other animals exhibiting alternation are in great part sessile organisms, attached to their substratum. But when a fixed organism propagates itself and distributes its kind, it must commit portions of itself to the winds or to currents of water, if new regions are to be occupied; a condition applying equally to plants and animals. Or, as an alternative, sexually-produced progeny may be liberated from the mother-organism and take up new positions. But sexual reproduction amongst fixed organisms requires rather special arrangements, and even with their aid is not invariably certain. Interference with fertilization may connote the extinction of the species; consequently a propagation by asexual means is of great importance for such organisms. By a definite alternation of the two methods, by a single act of fertilizing leading to an organism capable of multiplying itself almost indefinitely by asexual spores, a numerous progeny is ensured even from a single sexual union. Take the case of the Fern-

prothallium; from one fertilized archegonium arises a Fern-plant with many fronds and capable of producing millions of spores. Thus the species, whilst retaining to itself such advantages as may be inherent in the sexual process, is likewise able to diffuse itself in large numbers over an extended area by means of its numerous asexually-produced spores.

Allusion has been made to the advantages inherent in the sexual process. The investigation of their precise nature will be one of the main problems reserved for the second part of this volume. That a production of flowers and a ripening of seed is not *absolutely essential* for the maintenance and distribution of plants, seems not improbable—judging from the considerable number of plants which do well and flourish without them.

THE HISTORY OF SPECIES.

1. THE NATURE OF SPECIES.

Definition of Species—Specific Constitution of Protoplasm.

DEFINITION OF SPECIES.

The history of plant species is founded on the history of individual plants given in the first section of this volume, more particularly on the results afforded by investigation into the processes of reproduction and propagation. It deals with the description of the species from its origin to its end, and also takes cognizance of the replacing of extinct species by new ones. The execution of this task is less easy than the representation of the life-history of the individual which can be deduced from direct observation and experience. It being possible to follow the course of even long-lived individuals, beginning with the origin of the embryo and following it through all its life's stages, the meaning of certain vital processes as, for example, the pollination of the stigmas and the germination of the seeds can be understood. The origin of most of our present species, however, which have arisen without the aid of man, is shrouded in mystery; it occurred in long past ages and we are obliged to fall back on conjectures which, however intelligent and however they may be supported by carefully weighed considerations, are still only conjectures after all. For purposes of direct observation we have only the fossil remains of earlier times and the species which are living at the present day. By comparing these with one another, and by inferring the nature of extinct forms from that of living species, we are able to construct a chain of conclusions which after all may be regarded as the best available substitute for a history of species.

The most important foundations for these conclusions are afforded by the knowledge of the relations of living species to their environment, especially the recognition of those causes which bring about permanent changes of form, for this alone can elucidate the question of the origin of new species. Before discussing these important questions the nature of species must be described and we must understand exactly what is meant by a species.

The definition of a species was first introduced into science by Linnæus, and the Latin word "species" owes its origin in this sense to the great master of Botany. Linnæus laid down that each species consists of similar individuals which are related together by their origin, and which are the unaltered descendants of a common ancestor or pair of ancestors. It does not affect the value of the

definition that Linnæus considered these ancestors to be creations of the "*infinitum ens*"; but it is very important that he recognized existing organisms as the continuation, the rejuvenated portions of one and the same living being, so that the species is not a figment of the human mind, but is something which actually has an objective existence.

Moreover, to decide which individuals are similar, *i.e.* of the same species, we take note of characters apparent to our senses, especially of the form and structure of the plant-body. Each species has its special features or characteristics, and all individuals possessing these specific marks are said to belong to the same species. Specific characteristics are hereditary, and are transmitted unaltered to the descendants. There are, however, some plant characteristics which are not inherited, but which may appear or not according as the individual develops in this or that place, and these must be regarded as the expression of certain external conditions which have an influence on plant-organization. They form the foundation for the existence of the variety, according to Linnæus. The individuals of each species may vary, but the variations are not handed down to posterity; they change according to position and other external influences. Systematic Botanists since the time of Linnæus have therefore to consider two kinds of distinguishing marks or characteristics: (1) those which are inconstant and not inherited; and (2) those which are constant under widely different external conditions and are hereditary. The latter determine the species, the former the variety. Each species may exhibit several varieties at one time, but its specific characteristics remain unaltered. If the specific marks should have undergone any alteration in the descendants, these will form a new species, or rather the appearance of an individual furnished with new specific marks forms the starting-point for a new species.

The relations of outward form and structure relied on by systematic Botanists in the identification of plant species depend of course on the plan of construction of the protoplasm of the species in question, and again only the specific constitution of the protoplasm determines this constructive plan. Before we can arrive at a correct idea of the nature of species, therefore, it is above all things necessary to obtain as clear a picture as possible of the relations of the protoplasm to the external visible form.

THE SPECIFIC CONSTITUTION OF PROTOPLASM.

Mention has previously been made of the remarkable fact that the species of a genus differing from one another in outward appearance also differ in respect of the scents secreted by them. Many Roses have different scents (*Rosa alpina, arvensis, cinnamomea, Gallica, Indica, Nasterana, pomifera, rubiginosa, sepium,* &c.), and a blind man could distinguish each species by the scent of its flowers. This is also true of species the foliage, stem, and roots of which emit odorous substances. By rubbing the foliage of different species of Thyme in one's fingers

(*Thymus Chamædrys, montanus, vulgaris, Zygis*, &c.), each will give off a peculiar scent; and when the roots or root-stocks of different Valerians (*Valeriana celtica, dioica, elongata, officinalis, Phu, saxatilis*, &c.), or of different species of the Asarabacca genus (*Asarum Canadense, Europæum*, &c.) are dug up, though they all smell of valerianic acid or spikenard, each species has in addition a distinctive odour of its own. The edible Fungi (*Polyporus confluens, frondosus, ovinus*, &c.), Garlics (*Allium ascalonicum, Cepa, Porrum, sativum, Schœnoprasum*, &c.), various Currants (*Ribes alpinum, petræum, rubrum*, &c.), and the Strawberries (*Fragaria collina, elatior, grandiflora, vesca*, &c.) all demonstrate most decisively that our olfactory nerves can distinguish between the different species of some genera. It might also be pointed out that it is no infrequent occurrence for one species of a genus to be poisonous to man while another is harmless, *e.g.* species of the Star-Anise genus (*Illicium anisatum* and *religiosum*), and of the fungal genus Lactarius (*Lactarius deliciosus* and *torminosus*). It is familiar to naturalists how precisely herbivorous animals can distinguish between different species of plants. The caterpillar of the Oleander Hawk-moth (*Sphinx Nerii*) lives exclusively on the Oleander (*Nerium Oleander*), that of a small Mediterranean butterfly, *Thais Hypermnestra*, only on the Birthwort (*Aristolochia Clematitis*), that of the small Tortoise-shell Butterfly (*Vanessa Urticæ*) only on the leaves of the large Stinging Nettle, and that of *Libythea Celtis* only on the foliage of the Nettle-tree (*Celtis australis*). Each caterpillar can at once distinguish the only species which suits it from numerous other similar ones. A friend of mine once found the caterpillar of a butterfly he did not know high up on the Gletscherstock in the Stubai, Tyrol, which he took into the valley with him intending to feed it until it became a chrysalis in order to obtain the butterfly. In the valley he placed it on about a hundred different plants in the hope that it would settle on one or other and use it as food. But it would not touch one of them, although caterpillars apparently suffer from voracious appetites. My friend now determined to revisit the spot where he had found the caterpillar and to set it at liberty there. When he did so it at once crawled as quickly as possible to a certain plant (*Cardamine alpina*) and attacked it with great eagerness. Later he discovered it to be the caterpillar of *Pieris Callidice*, which only feeds on the small Alpine Bitter-cress (*Cardamine alpina*). Generalizing from these instances, many more of which might be given, we are justified in assuming that the aromatic substances, alkaloids, acids, &c., which are manufactured in the plant metabolism are quite definite for each particular species. But it is equally obvious that a specific protoplasm is necessary for the manufacture of specific substances, or, in other words, that each plant-species with a certain definite form possesses also a definitely constituted protoplasm of its own.

The behaviour of different species with regard to temperature is especially worthy of note among the many observations which support this view. It is well known that seeds of various species which closely resemble one another in outward appearance differ greatly in the temperature they require for germination. Seeds

of one species are content with a low temperature, while those of another require much greater heat, although the eye can distinguish no difference in the structure of their coat, in their manner of storing reserve food, or in the structure of their embryos. The same may be said of the freezing of plants. Many Californian and Mexican Pines (*Pinus*) are very like those of Northern and Central Europe, and yet the one will be frozen to death as soon as the temperature sinks below freezing point, while the other can sustain winter temperatures of −20° C. without injury. There seems to be no reason why the South European Junipers, *Juniperus Oxycedrus* and *phœnicea*, which are apparently of the same structure as the similar species *Juniperus nana* and *Sabina*, should not flourish equally well on our mountain heights in the Central Alps, where the latter cover whole mountain peaks and send their roots into ground which is covered with snow eight months every year, and is frozen hard for months together. The common Ivy (*Hedera Helix*) grows in Central Europe without any protection from the fairly severe cold of winter; the S. European Ivy, *Hedera poetarum*, which is very similar to the common species, but can be distinguished from it by several external characteristics, requires a protecting roof in the gardens of Central Europe if it is to survive the winter unkilled by the frost. The same is true of two closely allied species of Marigold, viz. *Calendula arvensis* and *fulgida*, the former growing in Central, the latter in Southern Europe. In 1874 I sowed seeds of *Calendula arvensis* from the Rhine district side by side in the same garden-bed with seeds of *Calendula fulgida*, which had been gathered in Sicily. Very luxuriant plants which flowered in profusion grew up from both kinds of seeds. The first frost in that year in the place where the experiment was made occurred on October 25th. *Calendula arvensis* was not injured; its foliage was fresh and green, and remained in this condition during the following days, although, until November 2nd, the temperature fell every night from −1·5° to −2·5° C., and in the morning the stem, leaves, and flowers were studded with hoar-frost. *Calendula fulgida*, on the other hand, was destroyed by the frost on the night of the 24th–25th October. Its leaves and stems withered and turned brown, and exhibited all the symptoms observable in death by freezing. In 1864 I found a *Cytisus* on the rocky shores of the Adriatic Sea at Rovigno, which closely resembled the wide-spread *Cytisus nigricans* of Central Europe, but which had certain distinguishing features. I named it *Cytisus australis*. Some of its seeds were collected, and from them strong young seedlings were obtained in the following year. These were planted in the Botanic Garden at Innsbruck with some seedlings of *Cytisus nigricans* of the same age from the Danube valley, near Mautern, in Lower Austria. Both grew under identical external conditions, and appeared to be equally vigorous. But during the winter the plants of the *Cytisus* from the shores of the Adriatic were killed by the frost, while those of the *Cytisus* from the Danube valley remained healthy and strong. The experiment was repeated with the two plants in the following year. Young plants were again raised from seed, but this time those from the Adriatic coast were protected against the cold, and in this manner they survived the winter without harm. Two years later both

the species of *Cytisus* developed flowers and fruits almost simultaneously under the same external conditions, and it was noticed that the same real, if insignificant, deviations were present in the external characteristics which had been present in the parents. This different behaviour of plants which, on account of their form, are described by the Botanist as distinct species, although closely allied, can indeed only be explained by assuming that the protoplasm, though having on the whole a similar constitution, is somewhat different in each species.

As a further confirmation of the assumption that the protoplasm of each species possesses properties which are lacking in that of others, we may take the case of the behaviour of pollen-cells in fertilization. If two kinds of pollen-cells are brought to the stigmas of a plant, *i.e.* pollen-cells of two different species, it usually happens that the one will fertilize the ovules with its pollen-tubes, while the other will be without effect. And yet the conditions are the same in both cases, and the difference in behaviour must therefore depend upon some difference in the protoplasm of the pollen-cells. Protoplasts which swim about as swarm-spores in the same drop of water, exposed to exactly the same condition of light, heat, pressure, &c., display a different behaviour if they belong to a different species. Those of one species will always twist to the right, those of another always to the left, some seek the light, others shun it for the darkest places. But since the protoplasm behaves differently under the influence of the same ray of light, the same temperature, and the same pressure, the cause must be sought for in the tiny mass of protoplasm of which each swarm-spore is composed.

The little amœbæ which proceed from the spores of Myxomycetes are protoplasts without a cell-wall; they live on dead parts of plants, where they feed, grow, divide, and multiply. When the right time comes these amœbæ fuse together to form a body known as a plasmodium, which is ultimately converted into a mass of sporangia (*cf.* vol. i. p. 572). Although the little amœbæ of different species cannot be distinguished from one another, and the plasmodia look like masses of formless protoplasm which only differ sometimes in colour, the resultant sporangial forms exhibit a remarkable variety of forms. From the plasmodium of *Stemonitis fusca* there arises a network of dark brown threads which is penetrated by and borne on a central axis like the shaft of a feather (see figs. 355[1] and 355[2]); from that of *Spumaria alba* is formed a white slimy mass resembling the "cuckoo-spit" of the Cicadellidæ and enveloping stem and leaves just in the same way (see fig. 355[3]); from the plasmodium of *Dictydium cernuum* there arises a globe-like lattice-work with strong longitudinal ribs and delicate cross-bars, which is carried on a hooked stalk (see figs. 355[4] and 355[5]); from the formless plasmodium of *Craterium minutum* arise stalked cups of a gray colour (see figs. 355[6] and 355[7]); from that of *Arcyria punicea* short stalked conical bodies not unlike Strawberries (see figs. 355[8, 9, 10]); the plasmodium of *Lycogala epidendrum*, which penetrates the wood of dead tree-trunks, forms balls of the colour of red-lead, about a centimetre in diameter (see fig. 355[11]), and out of the plasmodium of *Leocarpus fragilis*, which spreads over dead branches and twigs, proceed stalked egg-shaped sporangia, with

...e brown coats (see fig. 355 [12]). And all these peculiar forms arise under similar ...ernal conditions from apparently similar slimy and formless masses of proto- ...sm.

The same thing occurs in the Mushroom and Toadstool Fungi (Hymeno- ...cetes) which develop in the mould of the forest ground and on the dead bark ...tree-trunks. The mycelium is a network of white threads and strands, and ...ther the form of the colourless elongated cells composing the network nor

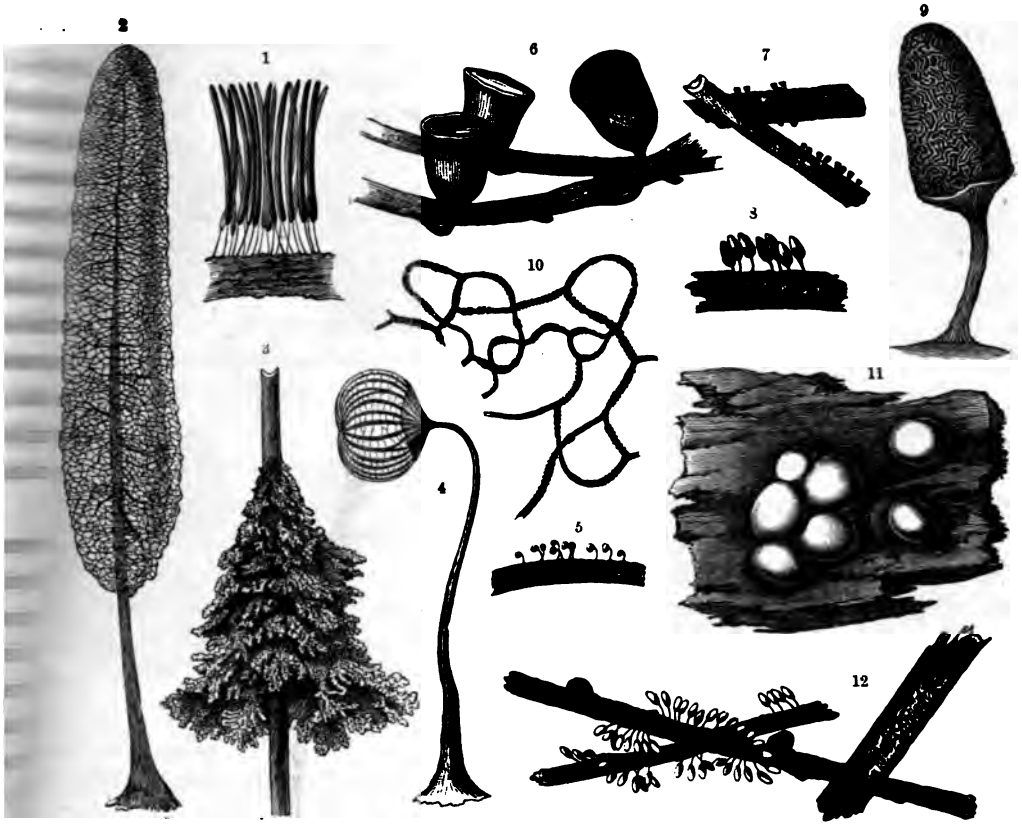

Fig. 355.—Myxomycetes.

[2] A group of sporangia of *Stemonitis fusca*. [3] A single sporangium; × 6. [8] Dendritic mass of sporangia of *Spumaria alba* on a Grass leaf. [4] Sporangium of *Dictydium cernuum*; × 25. [5] A group of sporangia of the same. [6] and [7] Sporangia of *Craterium minutum*; [6] × 25. [8] Sporangia of *Arcyria punicea*. [9] A single sporangium; × 10. [10] Part of the net-like capillitium of the same; ×160. [11] Fructification of *Lycogala epidendrum* on a piece of wood. [12] *Leocarpus fragilis*; a plasmodium on the right; several sporangia on the left.

the protoplasm within the cells afford any indication by which we can judge the species to which the mycelium belongs. But how different are the fructifications proceeding from these apparently identical mycelia. In a part of the forest ground not twenty paces across there grow large specimens of *Boletus edulis* with chestnut-brown hemispherical caps; a little distance off a group of Chantarelles (*Cantharellus cibarius*), with yellow colour like yolk of egg, close by the Fly-agaric (*Agaricus muscarius* or *Amanita muscaria*), with snow-white stipe and crimson cap (*pileus*) spotted with white, and near at hand, from

a mycelium which has penetrated the bark and wood of a Beech-tree, grows the horse-shoe-shaped ashen-gray *Polyporus fomentarius*—to mention but a few of the commonest forms.

The fruits resulting from the conjugation of the unicellular Desmids are minute balls of protoplasm, and although they may originate from very different species, outwardly there is not the slightest distinction between them. But as soon as these small balls of protoplasm begin to develop, the greatest variety of cell-forms is the result. Each is fashioned after the form of the parent individuals which produced the fruit by conjugating. One cell will be half-

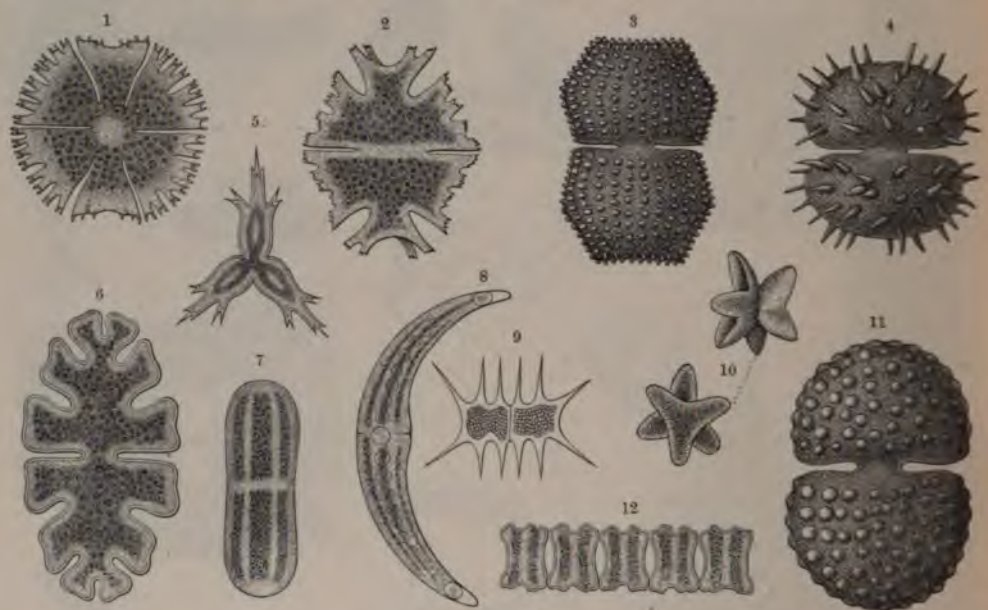

Fig. 356.—Desmidieæ.

1 *Micrasterias papillifera.* 2 *Micrasterias morsa.* 3 *Cosmarium polygonum.* 4 *Xanthidium aculeatum.* 5 *Staurastrum furcatum.* 6 *Euastrum oblongum.* 7 *Penium Brebissonii.* 8 *Closterium Lunula.* 9 *Xanthidium octocorne.* 10 *Staurastrum alternans* (two views). 11 *Cosmarium tetraophthalmum.* 12 *Aptogonum Desmidium.* All the figures magnified about 200 times.

moon-shaped, another cylindrical, a third angular and table-shaped, others again stellate and with manifold projections; some have a smooth surface, while the cell-wall of others is beset with spines or studded as if with pearls. The figures above, representing twelve different species of these Desmids, will give some idea of the multiplicity of their forms. And all these varieties spring from apparently identical masses of protoplasm, and develop side by side in the same drop of water, under the same illumination, the same temperature, and, generally speaking, under exactly the same external conditions and stimuli.

All these observations and results seem to indicate that the hypothesis as to a specific constitution of the protoplasm in each species is almost a necessary assumption. The word "constitution" has been purposely used instead of "composition", which might be taken to mean essentially the same thing were

dealing merely with a chemical compound. Nothing would be more natural than a comparison with inanimate things whose outwardly perceptible features are the expression of a definite chemical composition, *i.e.* of a certain grouping of molecules and atoms which can be represented by a certain formula. But although this comparison is allowable in general, yet there is an essential difference between mineral and plant species. No formula can be given for the protoplasm of a species of plant, and the structure of a protoplast cannot be compared with that of a crystal. Each protoplast represents an organism which contains very many chemical compounds. It is able to renew them when required, and to modify their grouping as dictated by external stimuli. With these displacements there must of course be a temporary alteration of structure, *i.e.* of the grouping in the formed part of the protoplasm. But all these displacements and alterations take place in each species according to the same plan. The same chemical compounds, the same aromatic bodies, the same acids and the same alkaloids, &c., can alone be demonstrated. The recently-formed parts agree with those already present, and merely fill up the places previously assigned to them. This unalterable law of form which governs the working of the protoplasm in each species is, therefore, dependent on some structure of the protoplasm which is beyond the perception of our senses, and it is this which is termed the *specific constitution of the protoplasm*.

In the above-mentioned Desmids, which afford such especially instructive examples, and in numerous other unicellular plants where all the formative processes are carried on within a single protoplast, it is easy to see the connection between the outward appearance and the specific constitution of the protoplasm. It is more difficult in species where there is greater division of labour, a division into manifold cell-forms and a gradual succession of different members. One might compare the processes occurring in them with similar processes in mineral species, which, with the same chemical composition present a great difference in their outward form and appearance. Carbonate of lime, which forms the mineral species *calcite*, appears in four kinds of crystal-forms, but they all belong to the same system, and can be derived from one another. In the same way the varied cell-forms and tissues, as well as the cotyledons, foliage, and floral-leaves, which arise from the same plant in regular succession, are to be regarded as members of the same system, succeeding one another in definite rule, although the specific constitution of the protoplasm in the particular species undergoes no change.

At one time the idea was prevalent that there are two kinds of protoplasm, *idioplasm* and *cytoplasm*. To the former was assigned the formative activity, while the latter was regarded as merely a nutritive plasm or medium. Subsequently it was shown that in every protoplast there is a more definite part, termed the *nucleus*, which dominates the whole, especially in the building and renewal of the cell-wall, while it also takes a leading part in cell-division and multiplication. Thus the assumption that all formative processes are carried on through

the cell-nucleus was held to be correct. The fact of the constancy of species from generation to generation was therefore referred, especially, to the specific constitution of the cell-nucleus. Since the nucleus plays such an important part in the process of fertilization, which precedes the inception of the new individual in sexual reproduction, the hypothesis was put forward that the constancy of form in the offspring, or, in other words, the transmission of form, depends upon the specific constitution of the nuclei taking part in this process. Nor would this hypothesis be open to objection had not recent investigations shown it to be extremely probable that portions of the male cell other than the nucleus assist at this process. If, as it appears, more than the mere nucleus passes over from the pollen-tube at fertilization (*cf.* p. 417), how can we certainly allege that (to take a definite case) all the properties which the young plant inherits from its male parent are transmitted through the medium of the nucleus? If it be true that a certain portion of the cell-protoplasm takes part in this act, it must be proved that it plays only a subordinate part in the process (*e.g.* a nutritive function) before we can attribute to the nucleus the part of sole carrier of transmitted properties.

To the proposition that new individuals with the unaltered properties and characteristics of the species can only spring from the protoplasm of this nucleus, we cannot assent. Thousands of plant-species reproduce asexually in unaltered form by spores and other offshoots. As already stated so often, every young cell of a plant may be the starting-point of an offshoot or brood-body, and so may lead to the beginning of a new individual; and an individual produced in this way bears all the characteristics of the parent plant which produced the offshoot. It might even be asserted that the features of the species are more certainly inherited in the case of reproduction by offshoots and brood-bodies than in sexual reproduction, and in a subsequent chapter it will be shown that it is sexual reproduction alone which affords the possibility of posterity with altered characteristics.

The view that the part surrounding the nucleus of a protoplast, the cell-protoplasm or *cytoplasm*, has no formative importance is not borne out by the evidence of investigations into the origin of the so-called galls, which we shall discuss in detail later, nor by our knowledge of hybrids. On the contrary, hybridization causes not only an alteration of form in the new individual arising from the germ-nucleus, but also an alteration in the form of the tissue in the region of the ovule exclusively influenced by the cytoplasm, so that the effect of hybridization can be recognized even in the fruit which arises from the ovary. Every influence on the cell-nucleus must be transmitted through the cytoplasm. But it would be much more difficult to imagine that the cytoplasm remains quite indifferent to this transference than that it also experiences a change identical with or similar to that undergone by the cell-nucleus. Fortified by these considerations, we may then assume (1) that all protoplasts which we know are able to form the starting-points of new individuals have the capacity of transmitting the external form of the species unaltered to the offspring, and (2) not only a part

but the whole of the protoplasm of any species possesses the specific constitution of that species.

It is of the greatest importance not only for the existence of the species, but also for the origin of new species, that the protoplasm, by reason of its specific constitution, should always take the same form. New species can only arise from those already in existence. This is equivalent to saying that the protoplasm of an existing species must undergo alterations in its constitution. Living protoplasm with new specific constitution must be produced from what already exists. How such a fundamental alteration is effected can only be guessed at by roundabout methods. One has to be content, as in so many other instances, with the results of experiment and experience, and with ascertaining, above everything, what influences are capable of altering the outward form of a whole or part of a plant either temporarily or permanently.

2.—ALTERATION IN THE FORM OF SPECIES.

Dependence of Plant Form on Soil and Climate.—Influence of Mutilation on the Form of Plants.—Alteration of Form by Parasitic Fungi.—Alteration of Form under the Influence of Gall-producing Insects.—Origin of New Forms by Crossing.

DEPENDENCE OF PLANT FORM ON SOIL AND CLIMATE.

The little town of Kitzbühel, in the North-east Tyrol, has a very remarkable position. On the north rises the Wilde or Vordere Kaiser, a limestone chain of mountains with steep, pale, furrowed sides, and on the south the Rettenstein group, a chain of dark slate mountains whose slopes are clothed far up with a green covering. The contrast presented by the landscape in its main features is also to be seen in the vegetation of these two mountain chains. On the limestone may be seen patches of turf composed of low stiff Sedges, Saxifrages whose formal rosettes and cushions overgrow the ledges and steps of the rugged limestone, the yellow-flowered Auricula, the Rock-rose-flowered Rhododendron, and white-flowered Cinquefoil adorning the gullies, dark groups of Mountain Pines bordered with bushes of Alpine Rose; and opposed to these, on the slate mountains, are carpets of thick turf composed of the Mat-grass sprinkled with Bell-flowers, *Arnica montana* and other Composites, groups of Alpine Alder and bushes of the rust-coloured Alpine Rose—these are contrasts in the plant-covering which would strike even a cursory observer, and would lead a naturalist to ask what could have been the cause. No wonder that the enthusiastic Botanist, Franz Unger, was fascinated by this remarkable phenomenon in the vegetable world. In his thirtieth year, furnished with a comprehensive scientific training, he came as a doctor to Kitzbühel, and with youthful ardour he used every hour of leisure from his professional duties in the investigation

of the geological, climatic, and botanical conditions of his new locality, devoting his fullest attention to the relations between the plants and the rocks forming their substratum. The result of this study was his work, published in 1836, *On the Influence of Soil on the Distribution of Plants as shown in the Vegetation of the North-east Tyrol*, which marked an epoch in questions of this sort. The terminology introduced in the book found rapid entrance into the Botanical works of the time. Unger divided the plants of the district according to their occurrence on one or other of the substratums—in which lime and silica respectively predominated—into (1) those which grow and flourish on limestone only; (2) those which prefer limestone, but which will grow on other soils; (3) those which grow and flourish on silica only; and (4) those which, whilst preferring silica, will grow on other soils. He tabulated his results in such a way as to show clearly how certain species grew on the limestone and others on the silica-containing rock. Naturally these facts elicited a number of speculations. If the species *Gentiana Clusii*, *Hutchinsia alpina*, and *Juncus monanthos* growing on the limestone soil are replaced on the slaty soil by the similar (but yet distinct) species, *Gentiana acaulis* (*excisa*), *Hutchinsia brevicaulis*, and *Juncus trifidus*, we are justified in assuming that the difference in form is due to the influence of the substratum, *i.e.* to the influence of the chief materials in the rock—limestone and silica. But it has yet to be ascertained and proved, if possible by experiment, how this influence works; whether limestone and silica, respectively, introduce certain compounds into a plant, thus altering its outward appearance, or whether the difference is due rather to the fact that each plant-species requires so much lime or so much silica, and that when this is lacking in the soil the outward form becomes changed; or again, whether, after all, the physical properties of the substratum, its porosity, capacity for retaining water, and its specific heat, have not more influence on the form of plants than its chemical constitution.

Unger and his followers, amongst whom I enroll myself, thought they would obtain an answer to these questions by comparing the chemical composition of the plant-ash with that of the soil in which the plants were grown. But the results of careful investigations were anything but satisfactory. Both the substances named, the presence of which was supposed to be of special importance, could be demonstrated in most of the soils examined. Labrador felspar, hornblende, and other minerals in crystalline slate yield as much lime in the upper soil as is required by plants demanding or preferring limestone (classes 1 and 2, above), whilst the Limestones, which almost all contain clay, have silica enough for the needs of plants which demand or prefer silica (classes 3 and 4, above). Moreover, it was shown that plants have the power of obtaining materials which are valuable to them even when these occur around their roots in hardly appreciable quantity, so that they actually become accumulators of certain materials, and in this way a substance of which there are only minute traces in the underlying rock may be relatively abundant in the superficial layers of soil impregnated with the d[illegible] plant-remains (*cf.* vol. i. pp. 70 and 259).

Under these circumstances it is a matter of indifference whether 10 per cent or only traces of lime or silica can be demonstrated in the soil, and the hypothesis that plant-species which grow on limestone fail to grow on slate because they are not able to supply their need of calcium, or that the plants growing on slate cannot flourish on limestone mountains because they cannot obtain the necessary amount of silica, must be abandoned, as well as the assumption that these substances when absorbed as food serve as a stimulus to change of form.

I strongly supported this latter hypothesis at the time, and thought I should be able to strengthen and confirm it by careful cultural experiments. Seeds of several species which demand lime were sown in soil containing hardly perceptible quantities of lime, and the seedlings were watered with water devoid of calcium; in another place seeds of species demanding a silica-containing substratum were placed in soil which contained much limestone, and the seedlings were watered with lime-water. At first it seemed as if an alteration of form had actually taken place in some individuals. But this was a mistake, or rather, the alteration only consisted in the greater or less luxuriance of the foliage, lengthening or shortening of the stem, abundant or scanty development of flowers and the like. But no actual change of form which would be retained by their descendants could be obtained. The species of plants accustomed to lime, grown on a soil devoid of lime, presented a miserable appearance, with scanty flowers which ripened only a few seeds, whilst the silica-demanding species grown on lime-containing soil soon withered and died without flowering at all. The change of form, indeed the actual interchange I had anticipated between the closely allied species which grow on the two rocky substrata in a state of nature, did not occur at all.

If we still take the case of siliceous and calcareous plants, and regard the soil as the source of free inorganic substances which influence the plants, we are forced to assume that greater quantities of one substance will be injurious to one or other of them. The absorbent cells have the capacity of choosing between the substances at their disposal, but this capacity has a definite limit in every species. The cells can absorb as much as they require from a very weak solution of common salt, soda, gypsum, calcium bicarbonate, &c., but a concentrated solution of these salts may injure and destroy their structure and function. If it is allowed to act for any length of time on the cells whose function is to absorb inorganic nutriment, the death of the whole plant will inevitably result. If the Moss which grows on blocks of granite is watered with a saturated solution of gypsum; if the soil into which our Meadow-grasses send their roots is watered with a saturated solution of common salt; or if the humus in which the plants of an upland moor grow is mixed with sodium carbonate or calcium bicarbonate, the plants invariably perish, and the same mineral substances, which in a very weak solution are needful, or at any rate harmless, become poisonous when the solutions are concentrated. The fact that one species of plant prefers this and another that mineral substance (see vol. i. p. 73), however, renders it probable that the injurious effect of materials in large quantity in the soil varies, that a large quantity of

common salt would be injurious to one species, and an abundance of sodium or potassium salts to another. From the present standpoint of our knowledge concerning the absorption of inorganic materials by plants, therefore, Unger's classification, especially the expressions silica-demanding and silica-preferring, is no longer suitable, and it would be more to the purpose to speak of plants which are injured by lime, potash, &c.

The difference in the vegetation on the closely adjoining limestone and slate mountains met with in so many places in the Alps, and so well seen in the neighbourhood of Kitzbühel, where the climatic influences on the two ranges are identical, can be accounted for most satisfactorily in the following way. Plant-species which demand or prefer a siliceous soil are absent from limestone mountains wherever their roots would be exposed to more free lime than is beneficial; if present they would be weakened, and thus vanquished in the struggle with their fellows, to whom the larger quantity of lime is harmless, and they would eventually perish. These plants flourish luxuriantly, however, on slate mountains, because there the soil does not contain an injurious amount of lime. The absence of species, demanding or preferring lime, from slate mountains can be explained in the same way. When seeds are brought thither by the wind from the neighbouring limestone mountains and germination commences, their further development is visibly retarded; they dwindle wherever there is not much lime, and are overgrown and suppressed by the siliceous species which flourish there so luxuriantly. The brown or black mass formed by the decomposition of dead plant residues, known as humus, plays a very important part in the contrasting vegetation on limestone and slate mountains. To obtain a true idea of its significance it must first be pointed out that three distinct stages can be distinguished in the development of a continuous and intricate plant-covering. To the first stage belong the plants which settle down on the bare earth content with a substratum wholly devoid of humus; in the course of time they conquer the most barren rock, the barest boulders, and the dreariest shifting sands. The species of this group belong chiefly to the Lichens, Mosses, Grasses, Pinks, Crucifers, House-leeks, Saxifrages, and Composites, whose spores, seeds, and fruits are exceptionally well adapted for wind distribution, and can be transferred with ease to the steepest slopes and the most uncompromising crags. The second stage includes plants which require a moderate amount of soil mixed with humus; they establish themselves on the ground prepared by the first settlers, wresting it from them and taking possession, and then suppressing and overgrowing them entirely. These plants belong to very different families, whose distribution and establishment are effected in very many ways to be described subsequently. The third stage of development consists of plants for which the abundant humus stored up successively by the plants of the second stage is absolutely indispensable. Bog-moss, Lycopodiums, Sedges, and Heaths form the chief part of this stage. In the course of years the amount of inorganic material in the soil which supports the plants of the third stage continuously diminishes. Plants which require a large quantity of inorganic salts languish, and are, moreover

overcome by saprophytes which find a suitable habitat there and flourish in abundance. The decayed portions of Saprophytes contain relatively little inorganic material. No trace of lime (in particular) is to be found in their ash. In this way a superficial layer of humus is formed which actually excludes a large number of plants. The next deeper layer may contain a considerable quantity of inorganic salts, but they are valueless to plants rooted in the upper (humus) layer, as they cannot penetrate it. It has been shown by experiment that pure humus possesses the power of holding back materials which are soluble in water. It possesses this property to such an extent that if salt solutions are filtered through a layer of humus the water which escapes below is almost pure. It is therefore impossible for inorganic substances from the deeper layers of the soil, much less from the underlying rock, to reach the surface layer of humus in solution by diffusion; and if some mineral ingredients are not introduced by irrigation or flooding, the upper layer of soil consists of pure humus on which only saprophytic plants can flourish.

The formation of such layers of humus occurs much more easily and quickly on slate mountains than on limestone, because in the former the rock and the products of its decomposition retain water much better, and a uniform saturation promotes the development of humus, and also because on slaty soil the second stage of the development of the plant-covering consists of plants which require very few inorganic food-substances, and accordingly very few inorganic materials are yielded by the humus, which originates at the cost of the decaying portions of these plants. But a thick stratum of pure humus may also arise in course of time on limestone mountains. Only the soil must be uniformly moist in that spot, and neither sand nor mud must be deposited on it. If these conditions are fulfilled a deep humus will gradually spread itself over limestone rocks and débris in the third stage of development, the superficial layer of which will contain no trace of lime, but will afford an excellent soil for silica-loving plants (*i.e.* for those to which lime is injurious). The isolated occurrence of so-called siliceous or slate-plants on limestone mountains, even in the middle of a patch of plants which are characteristic of a limestone soil, may be naturally explained in this fashion.

The water which moistens the rock and soaks the soil has, apart from its mechanical action, the important function of opening up mineral substances and of forming solutions from which the absorbent plant-cells may take their choice. The atmospheric water which penetrates into the earth from above is especially valuable as a solvent on account of the carbonic acid gas it contains. It is immeasurably more valuable to every part of the soil which is riddled by the roots of living plants than the soil-water, so poor in carbonic acid, which collects on impervious strata of the soil and soaks upwards through the superficial layers.

The power of the soil to retain water depends mainly on the extent of breaking up undergone by the rock whose disintegration has formed the soil and upon the amount of clay which has arisen from this disintegration. But the amount of humus which in course of time has mixed with the disintegration and the decomposition products of the underlying rock is also an important factor, and thus very

complex conditions arise which render the estimation of the soil's capacity for retaining water very difficult. If permeable sandy soil, poor in humus, is deprived of ground water and is dependent for its moisture solely on the atmosphere, the plants growing in it will be retarded in their development if rain and dew are absent for any length of time, and their outward appearance will be altered by this restriction of growth. Annual plants subjected to a lack of moisture in the soil, just at the time when their growth should be at its maximum, show best how far these alterations will go. The stem-structures remain short, the foliage-leaves shrink to their smallest extent, and no lateral shoots are developed. Only a few, or perhaps only one, of the flower-buds mature; it is small, opens comparatively very early, and the whole plant has a dwarfed aspect. Annual plants of the Poppy (*Papaver Rhœas, somniferum*), Pheasant's Eye (*Adonis æstivalis, flammea*), Corncockle (*Agrostemma Githago*), Cornflower (*Centaurea Cyanus*), and common Groundsel (*Senecio vulgaris*) grown on a dry soil differ from plants grown in the same place, but in a damp year, to such an extent in the size of all their parts that at first sight they might be mistaken for other species. A clay soil which retains water is less exposed to danger of too great dryness, but if it is not mixed with humus, and therefore loosened, it has the disadvantage that the water it contains cannot take up the inorganic foods quickly enough and in sufficient quantity for the requirements of the plants. This drawback explains the surprising fact that plants grown on heavy wet clay soils have a dwarfed appearance exactly like plants growing on dry sandy soil. In regions liable to flooding by streams and rivers where not infrequently sandy and clay soils, in all degrees of porosity and admixed with humus in all possible proportions, are to be met with within a few yards of one another, certain species of plants are to be found growing near together in all imaginable degrees of size, *e.g. Aster Tripolium, Bidens cernua* and *tripartita, Polygonum lapathifolium, Rumex maritimus, Veronica Anagallis.* In places where the seedlings cannot find enough free mineral foods, in spite of the abundant moisture in the soil, the stem rises to some 3–8 cm.; in places which favour the absorption of food, to some 50–80 cm. We will describe only one species, *Veronica Anagallis*, more in detail. Plants of this species are found with stems 3–5 cm. high and 0·5 mm. thick, with foliage-leaves 6–12 mm. long and 5–6 mm. broad when fully developed. The number of flowers in one inflorescence is about 4–5, the calyx and ripe capsular fruit measure 3 mm. in length. Contrasting with these are plants with stem 30–50 cm. high and 7–8 mm. thick, whose fully-formed leaves are 80 mm. long and 35 mm. broad. There are 40–50 flowers in each inflorescence, and the calyx and ripe capsule measure 4–5 mm. in length. Generally speaking these plants are about ten times as large as the others. If the soils which give rise to such surprising differences in size are examined it will be noticed that the dwarfed specimens are rooted in a heavy soil devoid of humus, while the large luxuriant plants flourish in a clay soil which is mixed with plenty of humus, and is therefore very open. Obviously the plants could not obtain from the heavy clay soil what they required for the structure of a vigorous plant, even although the

ground was well moistened and warmed; but this they could obtain in abundance from the saturated clay soil containing the humus.

It has been already stated that the ground water is less favourable for vegetation than rain and dew on account of its paucity of carbonic acid. But the moistening of the ground by water which wells up from below brings other evils in its train. By this means the soil is over-saturated for a long time, a condition which the roots of most land-plants will not tolerate. When it remains stationary for a long while potassium and sodium salts, and, under certain conditions, humous acids pass into it from the wet earth in quantities anything but advantageous to the plants. Vegetation, therefore, exhibits a scanty growth in places where the ground water influences the stratum of soil penetrated by roots, and it usually consists of comparatively few species.

In low-lying regions, where the ground water rises to the surface, we have the formation of lakes and ponds with variable water-level. Sometimes the plants growing in such places are quite submerged, while at other times their stem and leaves are above water. Land plants do not take kindly to this. Most of them cannot survive very long immersion; they become suffocated, die, and decompose under water in a few days. Only a few species have the remarkable power of growing equally well below or above water, and these are, of course, extremely interesting on account of their form. In accordance with the great contrast presented by the external conditions of life to which these species are temporarily exposed we have a fundamental change both in their outward appearance and in the internal structure of their several organs. In order that the stem and leaves should be held in the best position by the flowing water, the mechanical tissue in submerged varieties of these species is much reduced (see vol. i. pp. 424 and 665). They are also devoid of the contrivances which usually regulate transpiration, since no evaporation occurs under water. Stems grown under water consequently appear limp and flaccid when taken out of it; their leaves, when compared with those growing in the air, are much weaker and more delicate. They have no gloss, but are brighter green in colour, and in the air they collapse and dry up in a very short time. A vertical section through the leaf shows that the number of cells between the upper and lower epidermis is much reduced, and that the cells are shortened in a direction perpendicular to the leaf surface. The foliage-leaves of *Veronica Beccabunga*, when grown under water, are hardly one-third as thick as those grown in the air, and between the upper and lower epidermis there are only 4–5 layers of short cells, while in corresponding leaves of aërial plants there are 10–12 cell-layers and a distinct division into palisade and spongy parenchyma (see vol. i. p. 279). The shape of the leaf is also much changed under water. In *Veronica Beccabunga* the difference in aërial and submerged leaves is very slight, consisting only in the shortening of the petiole and in the marginal teeth becoming less marked. In *Veronica Anagallis*, likewise, the alteration in shape is inconsiderable, but in many others it is very noticeable, and we shall return to it when speaking of the influence of light.

Plants rooted in the mud of a river-bed, the stems and leaves of which are surrounded by rapidly-flowing water, must possess corresponding strength if they are not to be torn. In comparing two plants of the same species, the one growing in the still water of a deep lake, the other in a rapidly-flowing stream, it will be noticed that the walls of the superficial cells of the latter have become strongly thickened, and that strong bundles of bast-fibres have developed in the cortex of the stem, while in the former only the weakest traces of bast-fibres can be seen. The extraordinary length of stem, petiole, and leaf-blade is also very surprising in plants which grow in rapid water. The Pondweed *Potamogeton fluitans*, the Rushes *Juncus lamprocarpus* and *supinus*, the Grasses *Agrostis stolonifera* and *Glyceria fluitans* are very instructive examples. A plant of the last-named Grass growing on damp soil on the edge of a stream over the water had linear, bluntly-pointed leaves, whose sheaths were on the average 15 cm. long, the blades 23 cm. long and 8·5 mm. broad. After this plant had been submerged under rapidly-flowing water in the following year, leaves unfolded, which tapered gradually to a point, with a sheath having a mean length of 4·7 cm., and blades 73 cm. long but only 5 mm. broad. The blades produced in running water were three times as long and actually rather narrower than in the air. There was no difference in the number of strands traversing the blade, but they were nearer to one another than in the aërial leaves. The Arrow-head (*Sagittaria sagittifolia*), which usually grows on the muddy bottom of shallow lakes, raising its leaves above the still water, has gained its name from the likeness of its leaf-blade to an arrow. If it is planted in the bed of a rapid stream so that the leaves during their development are exposed to a vigorous current, the leaf-blade is almost entirely suppressed. What still remains has the form of a spade, but not infrequently all trace of lamina is wanting. The petiole, however, lengthens to 70 cm., and forms a limp, flat, pale-green ribbon 1–2 cm. broad, which might easily be mistaken at first sight for the leaf of *Vallisneria*.

Another remarkable change which is effected by submerging growing plants is the non-development of the epidermal structures called hairs, so that the leaves and stems of submerged plants always appear smooth. The suppression of hair-structures is very noticeable in the aquatic variety of *Polygonum amphibium*. In aërial plants of this species the leaves have short petioles, are lanceolate in shape, and are covered thickly with short hairs, which are rough to the touch; while the aquatic plants have long-stalked, broadly-linear leaves completely smooth on both sides.

The humidity of the atmosphere has a marked effect on the form of land plants. Transpiration, which is so deeply concerned in all the vital processes, is carried on very slowly in air which is almost or quite saturated with water-vapour. If plants of a species which usually grows in dry air come into a humid atmosphere, they must be furnished with means for aiding evaporation. On the other hand, plants which grow in dry air must be protected against excessive transpiration. The aids and protective measures were so minutely described

in vol i. pp. 284 and 307, that it is needless to repeat them here; but it should be noted that the capacity of plants to construct their tissue as need requires, either for aiding transpiration or for protection against excessive evaporation, is very limited. It must also be pointed out that it is very difficult to distinguish clearly between the direct effect of the humidity of the air and the effects of other influences. Heat and light, as well as the amount of moisture in the soil, are intimately connected with the humidity of the air, but the relations are difficult to estimate. To a certain extent they are interchangeable, and therefore, in most instances, it is impossible to say which external influence is the cause of any particular alteration in the tissue concerned in transpiration. For the answer to the chief question, whether it is possible for a change in the conditions of life to cause an alteration of form in the sense of an adaptation, it is really a matter of indifference which influence causes the visible effect. Only here, as in so many other cases, matters are simplified if a certain partiality is permitted in experiments for solving these difficult questions, and if the interwoven influences of soil and climate are treated separately.

The effect of heat on growing plants was discussed at vol. i. p. 523. It only remains to say here that the formation of starch and other reserve-foods, as well as the formation of sugar in fruits, is largely connected with heat. Fruits of the same species which ripen under a higher temperature differ greatly in the amount of sugar they contain from those ripening at a lower temperature. It is generally accepted that the size also of the stem, foliage, flowers, and fruit is influenced by heat. The changes which occur when plants in flower, after being for some time in a very warm room are transferred into a cooler room, the other conditions remaining the same, are in particular now recognized. When a large-flowered bulbous plant, *e.g.* the Belladonna Lily (*Amaryllis Belladonna*), is transferred to a cold greenhouse after opening its first flowers in a warm one, the flowers it here develops at a lower temperature are almost a third smaller than those produced in the warm house. But when the first flowers open in the cold, and the later ones in a warm atmosphere, the former remain small and the latter are larger in size. It is important to emphasize this circumstance in order that the phenomenon here exhibited may not be mistaken for another, in case we should be led to think that the flowers of a plant which first unfold are larger than those which succeed them even when there has not been the slightest alteration in the conditions of light, heat, humidity, &c.

It is particularly instructive, when examining the effect of heat on the form of a species, to compare plants grown in water of different temperatures but under conditions otherwise similar. In mountainous districts the springs on the same mountain slope have a different temperature according to their elevation, and yet the same species of plants may be found growing in springs at the foot and high up on the mountain. Let us take as examples plants of *Cardamine amara*, *Myosotis palustris*, *Pedicularis palustris*, and *Veronica Beccabunga*. These species grow at the foot of the Patscherkofel, near Innsbruck, in the bed

of streams with a mean temperature of 10·2 ° C., but they also flourish in a stream above the tree-line, at a height of 1921 metres above the sea-level, known as the "Kreuzbrunnen". Comparing plants of the same species growing under the influence of these different temperatures, the following differences are to be noted:— Plants of *Veronica Beccabunga* growing in spring water at a temperature of 10·2° C. were 20–50 cm. high, and displayed 4–6 internodes between the bottom in which they were rooted and the level of the first inflorescences. The internodes of the stem were 60–120 mm. long and 5 mm. thick; the leaves springing from the middle of the plant were 40–60 mm. long, 20–25 mm. broad, and each of the flower racemes had 12–16 flowers. Plants growing in the spring water at a temperature of 4·2° C. were 10–15 cm. high with 4–6 internodes between the ground and the level of the first inflorescences. The internodes were 15–30 mm. long and 10–12 mm. thick, and each inflorescence had 12–16 flowers. *Cardamine amara*, *Myosotis palustris*, and *Pedicularis palustris* behaved similarly. There seemed to be no alteration in the form of the leaves and flowers; the corollas assumed a rather deeper tint in the Kreuzbrunnen; *Myosotis palustris*, which was 20 cm. high at the foot of the Patscherkofel, was 4–5 cm. high in the Kreuzbrunnen, and closely resembled the *Eritrichium nanum* of the Southern Alps in the deep blue of its corollas. *Cardamine amara*, in the same cold spring, in addition to the shortening of its internodes and diminution of its foliage-leaves, displayed a red colour on the outside of its white petals which was not present in plants at lower levels.

The powerful influence of light on the development of plants was discussed at vol. i. p. 371. The question now before us is how far bright and subdued light are able to alter the size, form, and colour of plants. The following is a general review of what has been ascertained in the matter from experiments and direct observation of nature. When plants of a species develop in subdued light they always have higher stems and longer leaves than when grown in bright light, provided, of course, that the conditions of moisture and temperature have been as far as possible identical. This difference is especially noticeable in comparing two plants of a species, one of which has developed in the dim light of a greenhouse in the short days of winter, the other in an unshaded place in the open country during the summer when the light lasts for 16–17 hours every day. The former has a lank thin stem, delicate yellowish-green leaves, and either none of its flowers unfold or else they have a weak appearance and their corollas are pale and flaccid. The illuminated plant has, on the other hand, a compact vigorous stem, dark green leaves, and unfolds a multitude of bright-hued flowers. One only of the large number of experiments which have been performed for the purpose of determining this matter definitely will be mentioned here—one indeed which shows how far the form of the flowers also may be affected. Seeds of a biennial Saxifrage, *Saxifraga controversa*, which were sown in several flower-pots filled with similar soil, produced numerous young plants. A pot with six of these young plants was taken in the autumn into the hot-house; another, likewise containing

six young plants, passed the winter under a thick coat of snow in the open. At the beginning of December the six plants in the hot-house sent up from the centre of their small leaf-rosettes slender stalks 10 cm. high, whose upper internodes were 22 mm. long and 1 mm. thick. The stem-leaves were yellowish, entire, elongated, 6–7 mm. long and 2 mm. broad; calyx-tube 4 mm. long, 13 mm. broad; calyx-teeth 2 mm. long, 1·5 mm. broad; petals 3·5 mm. long, 2 mm. broad; stamens 1 mm. long. It was noted that lateral axes only developed in the axils of the upper stem-leaves, and that the buds of the lateral shoots in the lower leaf-axils atrophied. In the following May strong stems 6 cm. high were sent up from the leaf-rosettes of the plants which had wintered under the deep snow in the open; their upper internodes were 12 mm. long and 2 mm. thick. The stem-leaves were somewhat broadened in front with dentate margin, red in colour, 5 mm. long and 3 mm. broad. The measurements of the parts of the flowers were:—Calyx-tube, 2 mm. long, and 2 mm. broad; calyx-teeth, 1·5 mm. long, 1 mm. broad; petals, 2·3 mm. long, and 2 mm. broad; stamens, 1 mm. long. From the axils of the stem-leaves flower-bearing shoots developed, which, like the parts of the main stem exposed to the sun, were coloured red. Here then the alterations which certainly are due to the various light influences consist not only in the lengthening and shortening of the stem- and foliage-leaves, but the flowers are correspondingly changed. The petals of the flowers which opened at the New Year when the days were shortest were not only relatively but actually narrower than those which belonged to flowers which opened in the early summer when the days were longest.

It has already been stated that the elongation of the leaves and the division of the leaf-lamina into long narrow segments in submerged leaves is associated with the diminution undergone by the light in passing through the water (see vol. i. p. 665). The elongation of submerged leaves is very well seen in the water Starwort (*Callitriche*) and Mare's-tail (*Hippuris*). In the latter the linear submerged leaves are thirty times as long as they are broad, while the length of the aërial leaves is only 7–9 times their width. In *Roripa amphibia* the leaves which develop under water are deeply cleft compared with those produced in the air. The aërial leaves of this Crucifer are linear-lanceolate, about ten times as long as broad, with finely toothed margin. Under water the leaves have an elliptical shape, are 2–3 times as long as broad, and the lamina is cleft almost down to the midrib in narrow segments 2–3 cm. long, like a comb or feather. The aërial leaves of the whorled Waterwort (*Elatine Alsinastrum*) are grouped in whorls of three. They have an ovate shape, and their margins are finely notched. Each is traversed by 3–5 veins. The leaves developed under water are divided almost their whole length into 3–4 narrow linear segments, and each whorl looks as if it were composed of twelve leaves. Each segment is smooth round the edge, and traversed only by one central vein. The difference between the aërial and submerged leaves of the white-flowered Crowfoots (belonging to the *Batrachium* section of the genus *Ranunculus*) is even more surprising. Plants of these Crow-

foots which have developed on muddy but not inundated ground display three- or five-cleft leaves whose segments are light green in colour, shiny, and almost fleshy, and spread out flat. When these plants are grown under water the leaves appear quite different; they become divided into numerous thread-like or hair-shaped segments which have a dark-green colour, and the polished surface has entirely disappeared.

The shade afforded by stones, loose earth, undergrowth, and neighbouring bushes and shrubs acts on growing stems, foliage-leaves, and flowers just in the same way as the light-subduing layer of water. In a place near my country house which was formerly used for storing wood and dry twigs, but which had remained unused for a long time, the Creeping Thistle (*Cirsium arvense*) had established itself and formed an intricate growth. The crowded stems attained a height of 80 cm. at the time of flowering and fruit ripening. In the winter of 1885 wood was again stored there in piles 150 cm. high. When, early in the following summer, the new shoots of the Thistle began to spring up they were obliged to content themselves with growing through the dark chinks between the blocks of wood. Many were thus forced to bend and twist, and finally came against some insurmountable obstacle so that they dwindled in the crevices of the wood-stack without ever reaching the light. Others again which were able to find a fairly straight road through the crevices grew up until they reached the surface of the wood-heap, they then continued to grow 50 cm. higher and unfolded large foliage-leaves on this upper portion. They also developed branches with flower-heads, and from a distance it looked as if a group of Thistles had grown on the top of the wood-stack. The stems had attained a height of 2 metres. The lower internodes were twice as long as usual, the foliage-leaves which sprang from the stalk inside the dark crevices were small, yellowish green, and the buds in their axils did not develop. The Cow-berry (*Vaccinium Vitis-Idœa*) behaves similarly when its shoots are obliged to grow up to the light through dead tree-trunks. Shoots which force their way in the dark between the bark and the wood of the trunk may reach the height of a metre, while neighbouring ones, springing directly from the soil of the forest are only 15 cm. high. The shoots inside the bark have a reddish colour, and they bear small pale scales instead of dark-green foliage-leaves.

From the creeping stems of the White Clover (*Trifolium repens*) spring erect petioles terminating in three leaflets, and an erect angular stem bearing a flower-head. In sunny places, especially where no neighbouring plants cast a shade, the petioles reach a length of 8 cm., and the stem of 10 cm. But if dense bushes overshade the Clover, the petiole and stem elongate until the leaflets and capitulum they bear reach the light. Under these conditions petioles 28 cm. long have been found, and stems attaining a height of 55 cm. An extraordinary elongation also occurs in the radical leaves of the Dandelion (*Taraxacum officinale*) in places where high Grasses and thick bushes shade the moist soil. In the open the leaves reach a length of 20 cm., but in the shade they become twice or three times as long. The lower part of the leaf lengthens most, the free end is comparatively

very little altered, and in the central portion the only change is that the lobes and teeth become shorter and less clearly marked.

In order to ascertain the effect of covering plants with earth, numerous bulbs of a species of Tulip (*Tulipa Gesneriana*) were planted at the same depth in one garden bed, and in another some corms of the Spring Crocus (*Crocus vernus*). Earth was heaped over these bulbs and corms in successive heights of 5, 10, 15, 20, 25, 30, 35, 40, 45, and 50 cm. Naturally the leaf-tips and flower-buds were first seen in the places where the bulbs were only covered with 5 cm. of soil; in both beds the development was delayed—in the other cases in proportion to the height of the soil above the bulbs. Some flower-buds of the Crocus appeared above the 20 cm. of soil, one of the Tulip above the 30 cm. Numerous leaf-tips of the Crocus appeared above the 35 cm., and a few of the Tulip above the 40 cm. of soil. The perianth-tube, the peduncle and the foliage-leaves were almost twice as long as those which had developed under only 5 cm. of soil. The flowers were smaller, and unfolded just above the soil; the leaves were narrower and pale yellow in colour as far up as they were covered with the soil. Neither the Crocus nor the Tulip raised their leaves higher than 40 cm. Apparently the reserve-materials stored in the corm and bulb-scales were not sufficient for a further elongation. The stems and leaves of the Crocus and Tulip thus exhibit alterations similar to those observed in the sprouts of Potato-tubers in a dark cellar.

We should expect that if moisture and lack of light produce elongation of shoots and various alterations in leaves, a brilliant illumination would have the opposite effect on growing plants. This is indeed the fact. Plants which have been for a year in the shade and have been placed at the beginning of their development in the following year in the sun display shorter internodes and firmer leaves; they blossom more abundantly, the flowers are of a deeper hue, and in many cases a covering of hairs is formed over the green portions. It is not necessary to mention how far transpiration, which is much more active in the sun than in the shade, is concerned in this; these alterations are certainly produced in the end by sunlight.

The effect of brilliant illumination is best seen by comparing plants grown from similar seeds at different elevations, but under identical conditions in other respects. The results obtained in my experimental garden near the summit of the Blaser in the Tyrol, at a height of 2195 m., during the years 1875–1880 illustrate this very fully, and I will briefly recount them here. The seeds of some annual plants were sown in September. The beds were covered with a layer of snow a metre thick throughout the winter. The germination of the seeds took place in the following year soon after the snow melted between the 10th and 25th June. The seedlings therefore developed during the time when the sun was highest and the days longest, and the young plants were exposed to a temperature not lower but rather higher than that enjoyed by plants from similar seeds which began to develop in the experimental beds of the Vienna Botanic Garden in March, when the daylight lasted about 12 hours. The seedlings of several species (e.g. *Gilea tricolor*, *Hyoscyamus albus*, *Plantago Psyllium*, *Silene Gallica*, *Trifolium incarnatum*) were

killed by the isolated frosts which occurred in each of the six years of the experiment, not only in the last week of June, but during July and August; but others (e.g. *Agrostemma Githago, Centaurea Cyanus, Iberis amara, Lepidium sativum, Satureja hortensis, Senecio vulgaris, Turgenia latifolia, Veronica polita, Viola arvensis*) only underwent a short temporary stoppage of growth from this cause, and opened their flowers at the end of August and beginning of September. In the plants of some species (e.g. *Senecio vulgaris, Veronica polita, Viola arvensis*) ripe seeds capable of germinating were formed in September. The flowering specimens, in comparison with those which had grown during the short days of the spring exposed to numerous night-frosts in the Vienna gardens, displayed extremely shortened internodes. The number of internodes was also lessened, or rather, fewer were developed. For example, where 10 internodes developed in an experimental plant in Vienna, in the Alpine garden a corresponding plant would only have 5–6. The same was true of the development of the flowers. While in a plant of *Viola arvensis* in Vienna the axillary buds of the first six foliage-leaves were suppressed and flowers were not produced until the seventh and eighth leaves, flowers grew from the third and fourth axillary buds in the same species of plant grown in the Alpine experimental garden. The number of flowers on a plant was less, the petals were smaller on the average, and, generally speaking, the annual plants in the Alpine garden had the same appearance as those grown in the plain on dry, sandy soil described on p. 500. It has already been stated on p. 453 that some of the species which are annuals in the valley and on the plain do not die in the autumn in the Alpine garden, but remain alive through the winter and in the following year develop new shoots from the stem.

To describe the alterations undergone by biennial species in Alpine regions we will take *Libanotis montana* (an Umbellifer) as an example. Its stem in the Alpine garden was 16–24 cm. high and developed 5 internodes which were 2–5 cm. long. From the axils of the 5 green stem-leaves sprang lateral shoots which did not branch but terminated in a single umbel, so that the plant only bore 5 umbels altogether. The plants grown from similar seeds in the Vienna Botanic Garden exhibited a stem more than a metre high with 10 internodes each 10–20 cm. long. No lateral shoots were produced from the axils of the lower stem-leaves. Those from the axils of the middle and upper leaves were branched and bore several umbels. On an average a plant had about 20 umbels altogether.

Over 300 species of perennial plants were grown in the Alpine experimental garden. Only 32 of them blossomed, however. Those whose flowers usually precede the foliage-leaves were in full blossom at the beginning of July, the others, which had to develop a leafy stem before their flowers appeared at the top or in the axils of the leaves of this stem, did not flower until the end of August and beginning of September. Three species of the latter kind will be more particularly treated of here; one species whose stem bears only a single leaf and is terminated by a single flower (*Parnassia palustris*), one whose stem is beset with decussate leaves and terminates in a loose inflorescence composed of small cymes (*Lychnis*

Viscaria), and a third whose stem bears alternate leaves and whose flowers are grouped in capitula (*Pyrethrum corymbosum*).

The Grass of Parnassus (*Parnassia palustris*) from the Alpine garden, when compared with plants grown in the experimental beds of the Vienna Botanic Garden, showed the following measurements:—

	Vienna Botanic Garden.	Experimental Garden on the Blaser.
Height of stem	20–27 cm.	5–9 cm.
Dimensions of leaf	3·3 cm. long, 2·4 cm. broad.	1·0 cm. long, 0·6 cm. broad.
Diameter of flower	2·8–3·4 cm.	1·8–2·0 cm.

In the Alpine regions, therefore, the plant was only $\frac{1}{3}$ or $\frac{1}{4}$ as high and the leaves only $\frac{1}{3}$–$\frac{1}{4}$ as large as in Vienna, whilst the flowers in the Alpine region had a much smaller diameter than in Vienna.

Comparing the hermaphrodite plants of *Lychnis Viscaria* in the experimental garden of the Blaser with those of the same species at Vienna, we obtain the following:—

	Vienna Botanic Garden.	Experimental Garden on the Blaser.
Height of the stem, including the axis of the inflorescence	400–500 mm.	230–240 mm.
Dimensions of lower leaves	80 mm. long, 4 mm. broad.	50 mm. long, 3 mm. broad.
Inflorescence	80 „ „ 50 „ „	60 „ „ 40 „ „
Calyx	15 „ „ 6·5 „ „	13·5 „ „ 5 „ „
Lamina of petals	10 „ „ 8 „ „	8 „ „ 6·8 „ „
Claw of petals	8 mm. long.	7 mm. long.

Plants from the Alpine garden, therefore, when compared with those from the Vienna Botanic Garden, exhibit smaller measurements of stem, leaves, and flowers. The following points were also noted: the number of internodes in plants from the Vienna Garden was 9, of which 5 were on the axis of the inflorescence; each cyme consisted of 3–5 flowers, and the whole inflorescence bore 33–40 flowers. Plants from the Alpine Garden had only 6–7 internodes, of which 3 belonged to the inflorescence; the cymes composing the inflorescence were only occasionally 3-flowered; in most of them only the central flower developed, the two lateral ones being suppressed. The whole inflorescence included only 5–11 flowers.

Plants of *Pyrethrum corymbosum*, from the Alpine Garden, compared with those from the Vienna Botanic Garden (all raised from one batch of seeds) showed the following differences:—

	Vienna Botanic Garden.	Experimental Garden on the Blaser.
Height of the stem,	950 mm.	250 mm.
Dimensions of leaves,	170 mm. long, 50 mm. broad.	45–50 mm. long, 20 mm. broad.
Diameter of the capitulum,	26 mm.	20 mm.
Ray-florets,	8 mm. long, 4 mm. broad.	7 mm. long, 3 mm. broad.

In this case, again, plants from the Alpine Garden, when compared with those of the Vienna Botanic Garden, had smaller stems, leaves, and flowers. The lobes of the foliage-leaves from the middle of the stem of plants from the Alpine Garden were pinnate, and the pinnæ were either entire or beset with two small teeth on each side, near the apex. The stem had ten foliage-leaves, the four uppermost of which were much reduced and served as scale-leaves for the lateral shoots arising from their axils. These lateral axes were not branched, and each bore only a single capitulum. There were five capitula altogether. On plants from the Vienna Botanic Garden the lobes of the foliage-leaves from the middle of the stem were more divided, and the pinnæ were beset on each side near the top with 3–5 teeth. The stem bore 25–27 foliage-leaves, of which the 6–8 upper ones were much reduced in size, and functioned as scale-leaves for the lateral shoots in their axils. These lateral shoots were branched, and each branch terminated in a capitular inflorescence. The total number of capitula was 20–30.

From these examples it will be seen that all the parts of plants grown in the Alpine experimental garden were much hindered in their growth. The foliage- and floral-leaves were smaller, the stems shorter, the number of internodes, foliage-leaves, inflorescences, and flowers was diminished. The flowers were relatively nearer the earth, and this was due not only to the diminished number and length of the internodes of the stem, but principally to the fact that the flowers sprang from the axils of the lower stem-leaves.

Plants growing in Alpine regions derive a great advantage from these alterations, which are chiefly produced during their development by the influence of the long and bright daylight of June, July, and August. If these plants had to produce the same under-structure as their fellows in the Vienna Botanic Garden, 2015 metres lower down, much time would be lost, and the earliest flowers would hardly open before October, at a time when the winter snow is already beginning to fall. But since the number of internodes is restricted, and flowers are developed from the lower stories, it is possible for the plants to blossom at the end of August and beginning of September, and perhaps to ripen their fruits—one of the chief aims of the plant's existence. To this modification in their mode of development is also due in part the repeatedly-mentioned fact that many alpine plants blossom earlier than those in lower regions. But in order to avoid misunderstanding, it must be expressly stated that in not one of the thirty-two perennial, nor in the biennial and annual species which blossomed in the Alpine experimental garden, was the early flowering hereditary; consequently these plants must be carefully distinguished from the so-called asyngamic species, which will be spoken of in one of the last chapters in this book.

The relation of light to the colouring matters of plants has been repeatedly the subject of careful investigation. All observers agree that the amount of the pigment known as anthocyanin increases and diminishes with the stronger or weaker sunlight enjoyed by the parts of the plant in question, and that the yellow colouring matter of flowers holds a similar relation. Chlorophyll, however,

is actually destroyed by bright light in plants which are not properly screened, and the green tissue is then blanched and assumes a yellow tint. Since the intensity of the sun's rays increases with the elevation in mountain districts (see vol. i. p. 525), we should expect that this effect of light would be shown particularly well in plants of high elevation. And this is certainly the case. The flowers of species grown in the Alpine garden on the Blaser at a height of 2195 metres above the sea exhibited, as a rule, brilliant floral tints, and some were decidedly darker than the flowers grown in the Vienna Botanic Garden. *Agrostemma Githago*, *Campanula pusilla*, *Dianthus inodorus* (*sylvestris*), *Gypsophila repens*, *Lotus corniculatus*, *Saponaria ocymoides*, *Satureja hortensis*, *Taraxacum officinale*, *Vicia Cracca*, and *Vicia sepium* are good examples of this. Several species, which produced pure white petals in the Vienna gardens, *e.g.* *Libanotis montana*, had petals coloured reddish-violet by anthocyanin on their under sides in the Alpine garden. The glumes of all the Grasses which were green, or only just tinged with violet at a low level became a dark brownish-violet in the Alpine garden. The abundant formation of anthocyanin in the green tissue of the foliage-leaves and sepals, and in the stem, was particularly apparent. The leaves of the Stonecrops, *Sedum acre*, *album*, and *sexangulare* became purple-red, those of *Dracocephalum Ruyschianum* and *Leucanthemum vulgare* violet, those of *Lychnis Viscaria* and *Satureja hortensis* a brownish-red, and the foliage-leaves of *Bergenia crassifolia* and *Potentilla Tiroliensis*, even in August, had the scarlet-red colour which they usually assume in sunny spots in the valley in late autumn. I must not omit to mention that, according to some of my zoological friends, many animals, especially spiders and snails, which have been transferred from the plains to the mountain-heights, assume a darker tint in alpine regions.

A considerable number of plant species, especially those which grow in the valley in shaded or half-shaded places, as, for example, *Arabis procurrens*, *Digitalis ochroleuca*, *Geum urbanum*, *Orobus vernus*, *Valeriana Phu*, and *V. simplicifolia*, *Viola cucullata*, developed more or less yellowish leaves in the Alpine garden, where they were exposed to the full sunlight. It was mentioned in vol. i. p. 393, that the Flax (*Linum usitatissimum*), which flourishes in mountain valleys at a height of 1500 metres, where its chlorophyll is uninjured, nevertheless turns yellow in the Alpine garden at a height of 2195 metres.

From this general review of the modifications in plant-form obtained by culture-experiments, a series of important conclusions may naturally be drawn. In the first place we must point out that two kinds of characters are to be observed in plants, those which are the result of certain conditions and properties of soil and climate, and those which appear independently of these external influences. This distinction is so important that we shall illustrate it by two examples. The white Water-lily, *Nymphæa alba*, develops scale-leaves of ovate or lanceolate shape with no separation into petiole and lamina. The foliage-leaves, however,

have a rounded petiole and a disc-shaped lamina. These characters are always present whether the seed which produced the plant germinates in a deep lake or in the mud of a marshy meadow. In the marshy meadow the scale-leaves remain short, and the walls of their epidermal cells thicken in a remarkable way; the petioles of the aërial foliage-leaves become about a span long, and, in order to increase their resistance to bending, a strong layer of bast arises, the thickness of these bast-layers amounting to 0·17 mm. The walls of the epidermal cells are thickened, 5–9 layers of collenchymatous cells are formed under the epidermis with walls ·007 mm. thick, and the air-spaces in the centre of the leaf-stalk are much narrowed. But if this species of Water-lily grows under water, the scale-leaves elongate into long and flaccid ribbons, and the petioles of the foliage-leaves continue to grow until their blades are raised to the surface of the water. According to its depth they attain a length of 30, 40, 50–100 cm. Resistance to bending is but little required by the petioles, which are surrounded by water, and the bast is therefore only slightly developed. The strings of bast which traverse the leaf-stalk are only 0·11 mm. thick, the walls of the epidermal cells are only half as thick as in the aërial leaves, only 3–5 layers of collenchyma are developed below the epidermis and the air-spaces in the centre of the leaf-stalk have a diameter of over half a millimetre. These petioles are consequently flexible, and cannot support the leaf-blade if taken out of the water. The general form of the scale- and foliage-leaves, the segmentation of the latter into petiole and blade, the configuration of the blade and the distribution of the bundles in it are all the result of internal forces due to the specific constitution of the protoplasm; but the thickness of the epidermal cells, the strength of the mechanical tissue, and the length of the leaf-stalk, are determined by the depth of the water-covering. The same thing is seen in the flowers; their structure depends upon the specific constitution of the protoplasm, but the size of the petals is determined by the temperature of the water.

The Meadow-grass *Poa annua* has a rapid growth; its haulms and leaf-sheaths are round, the leaf-lamina is traversed by seven strands, the lower branches of the inflorescence are single or paired but never whorled, and the spikelets of the panicle are much compressed and egg-shaped in outline. These characters are unalterable and are observed in *Poa annua* under all conditions. But when the haulms growing in the gardens in the plain project beyond the short upmost leaf the spikelets become 6–7-flowered, and have a pale green colour. When the plants become perennial in alpine regions the haulms bend towards the ground and remain so short that they do not reach above the highest foliage-leaf; the spikelets develop only 3–4 flowers, and their glumes are dark violet on the surface and brownish-yellow at the edge; thus these modifications are in relation to peculiarities of situation (in the plain and alpine regions) as effect to cause, and are to be ascribed to the influences of heat, light, and moisture, which act in various ways according to the situation.

These alterations are always to the advantage of the plant. They make the

individual more resistant, support and protect its organs, and render it possible for the separate parts to perform their work in spite of the necessarily altered conditions. They seem to have the task of keeping the plant alive under very different vital conditions, of promoting growth and the formation of offshoots and fruit with the smallest possible expenditure, and they may therefore be regarded as adaptations to the particular conditions of soil and climate.

The capacity for adaptation is of course founded in the specific constitution of the protoplasm, and is very different in different species. One species may adapt itself by appropriate alterations to the influence of bright light, submersion under water, a dry atmosphere, &c., while another cannot do so. If the protoplasm of the Flax (*Linum usitatissimum*) could manufacture as much anthocyanin in its green tissue as the Summer Savory (*Satureja hortensis*) it would blossom and ripen its fruits in alpine regions as this plant does, and would not succumb to the effect of the strong light. If the protoplasm of the Common Bent-grass (*Agrostis vulgaris*) were able to continue its constructive activity under water it would not perish as soon as it is submerged, but would maintain itself like the stoloniferous species (*Agrostis stolonifera*) by green stalks and leaves adapted to an aquatic habitat. In short, the adaptability of each species is restricted within definite limits which depend upon the specific constitution of the protoplasm and cannot be overstepped.

It is a matter of great import in the history of species whether modifications in form effected by change of soil and climate are transmitted to the descendants, and whether they can be inherited. This of course can only be ascertained by experiments, and by experiments in which all possible sources of error have been eliminated. This last remark is made advisedly, for the sources of error in such experiments are very numerous. I will briefly indicate two which interfered with some experiments I carried out in the years 1863 and 1864. It is not enough to be careful that the seeds sown in the prepared experimental beds are all from the same plant; care must also be taken to see that they are not the result of a hybrid cross-fertilization. Some seeds taken in 1863 from a plant of *Dianthus alpinus* growing in the Botanic Garden at Innsbruck, and sown in different soil in two experimental beds, produced plants in soil free from lime, which, in their external appearance, agreed with *Dianthus deltoides*. It seemed as if *Dianthus alpinus*, a lover of limestone rock, had become transformed into *Dianthus deltoides* when grown without lime. The seeds of the plant so like *Dianthus deltoides* were again sown in soil without lime, but the resulting plants no longer resembled this species; they showed themselves to be constant in their characteristics. The whole experiment with *Dianthus alpinus* was then repeated, but this time the plants on the clay soil without lime did not change, and I was obliged to conclude that the plant I had regarded as a stage in the transformation of *Dianthus alpinus* into *Dianthus deltoides* was a hybrid of these two species. In order to be certain about this a crossing between the two species was effected artificially. From the resulting seed plants were actually grown which were exactly like those I had regarded as transformations, and there was no longer any doubt that some of the

stigmas of the *Dianthus alpinus* which had yielded the seeds for the first experiment had been pollinated by insects with the pollen of *Dianthus deltoides*.

Mistakes often arise also from the fact that the young stages of many plants are very different from the fully-grown specimens. Young Birches grown from the seeds of *Betula verrucosa* bear leaves which are simply serrated, thickly covered with hairs, and soft to the touch. They are deceptively like the leaves of adult plants of *Betula alba* or *pubescens*. The leaves of the adult *Betula verrucosa* have quite a different form; they are doubly serrated, smooth, and harsh to the touch. These latter are the only form of leaf described in Botanical books for *Betula verrucosa*. Anyone sowing the seeds from a grown tree, and watching them grow up, with leaves of a different shape and surface, might easily think an actual fundamental change had occurred, and might be tempted to regard the transformation as the direct effect of a change in external influences.

It is perhaps superfluous to state that due regard was paid to these possible sources of error in the later series of cultural experiments, carried out during six years in the Alpine garden on the Blaser (2195 metres), and for comparison in my Villa Marilaun in the high-lying Tyrolese Gschnitzthal (1215 metres), in the Botanic Garden at Innsbruck (569 metres), and in the Botanic Garden of the Vienna University (180 metres); *in no instance was any permanent or hereditary modification in form or colour observed.*

Seeds of a plant grown in the valley when sown in the Alpine region produced plants which exhibited the modifications described above. They were also manifested by the descendants of these plants *but only as long as they grew in the same place as their parents.* As soon as the seeds formed in the Alpine region were again sown in the beds of the Innsbruck or Vienna Botanic Gardens the plants raised from them immediately resumed the form and colour usual to that position. The modifications of form and colour produced by change of soil and climate are therefore not retained in the descendants; the characteristics which appear as the expression of these changes are not permanent, and the individuals are to be therefore regarded as varieties, of which Linnæus says in his *Philosophia Botanica*: "Varietates tot sunt, quot differentes plantæ ex ejusdem speciei semine sunt productæ. Varietas est Planta mutata a caussa accidentali: *Climate, Solo, Calore, Ventis*, &c., reducitur itaque in *Solo* mutato."

THE INFLUENCE OF MUTILATION ON THE FORM OF PLANTS.

When Birches and Firs grow up side by side in a wood-clearing, the crowns of the Birches will overtop the Firs in some twenty years' time, and this will seriously interfere with the growth of the latter. With every blast of wind the whip-like branches of the Birch strike against the upper shoots of the Firs, so that these gradually wither and die off. A lateral branch of a Fir tree altering its direction of growth and replacing the dead leader will, in its turn, soon be scourged to death. The top of the Fir is permanently mutilated, and the injury

can be recognized years after by the flattened form of the crown, so different from the usual appearance, when the offending Birches have perhaps long disappeared. Many other trees wage the same war with one another, the result in each case being the mutilation and alteration of the form of the summit of one of the trees. The Maple, for example, is either put quite *hors de combat* by the long thorny branches of a neighbouring Gleditschia (*Gleditschia triacanthos*) or else the crown becomes lop-sided owing to the destruction of the branches on the side facing the Gleditschia.

The way in which the appearance of Firs, Larches, Beeches, and Ling is altered by the attacks of ruminants, especially goats, was described in vol. i. p. 445, and we may add here that Pines and Junipers are mutilated in the same manner. The consequence is that lateral branches, which would not otherwise develop, grow out in the following year from the base of the twigs which have been bitten off. Apparently no other alteration takes place in these plants. But when huge boughs are broken off close to the ground by storms and the weight of snow, when the tree-trunks of the forest are sacrificed to the wood-cutter's hatchet, and the stems of seedling trees and shrubs in the meadow to the mower's scythe, when all the young shoots are frozen by a night's frost in spring, or when all the leaves are devoured by caterpillars and the branches are left bare as in winter—then the consequences are much more serious. In these cases new shoots make their appearance either from "eyes" in the stem or from the reserve-buds of the branches and twigs, or by buds produced by the roots below the ground. The leaves of these shoots, or *suckers*, as they are called, differ very much from those of the branches which have been broken, eaten, cut, or frozen off. The leaves from the crown of the Aspen (*Populus tremula*) are stiff and smooth in their adult condition; the circular blade is borne on a long petiole, and its margin is coarsely notched and undulated. The lateral veins traversing the blade are lost in a network near the edge in which no strong curved ribs occur. The leaves of a sucker from the base of a mutilated stem, or from the root, are soft and thickly covered on both sides with downy hairs; the heart-shaped blade is borne on a short stalk, and the margin is beset with numerous upwardly-directed notched teeth. The lateral veins of the blade merge near the edge of the leaf into a network, in which strong curved ribs are plainly visible. The leaves from the crown of the Oak (*Quercus pedunculata*) are deeply lobed and furnished with two so-called auricles at the base; those of the suckers are quite entire or very slightly lobed, with no auricles at the base. The leaves of the sucker of the common Beech (*Fagus sylvatica*) are more or less plainly serrated at the edge, while those of the topmost branches of the tree are quite entire. In the Black Mulberry (*Morus nigra*), and in the Paper Mulberry (*Broussonetia papyrifera*), the leaves of the sucker have a sinuous margin and are more or less deeply lobed, but those of the tree-top are heart-shaped with notched margins and no lobes. The leaves of the sucker of the Birch (*Betula verrucosa*) are simply serrated, with velvety hairs; those on the crown of the tree are doubly serrated and

smooth. The leaves on the suckers of the Round-eared Willow (*Salix aurita*) are broadly ovate, fairly smooth, and the veins in the blade form a wide-meshed reticulum; the leaves on non-mutilated branches are widened in the upper third, strongly wrinkled, and covered with grey hairs, whilst the reticulum of the veins is narrow-meshed. In *Salix rosmarinifolia*, the leaves of the suckers are twice or three times as broad as those of the normal branches, and they are smooth, while those of ordinary branches are covered with silky hairs, and gleam like silver. Hundreds of trees and shrubs might be mentioned in which there is a distinct difference between the foliage of the suckers and of the normal branches of the crown. But these few examples will suffice, and we will only mention the Norway Maple (*Acer platanoides*), because the difference in the foliage-leaves can be seen from the illustrations in vol. i. The leaves of the summit (see vol. i. fig. 106, p. 416, and fig. 109, p. 419) are borne on long petioles, the blade is 5-7 lobed, and the lobes are short and beset with several pointed, tapering teeth. The leaves of the suckers in this same Norway Maple are short-stalked, the blade is slightly 3-lobed, and each lobe is triangular and without the elongated pointed teeth. They exactly resemble the first foliage-leaves shown in vol. i. p. 9, fig. 1^1. This is also true of the leaves on the suckers of other woody plants. The shoots developed from reserve buds, "eyes", and the like, repeat to a certain extent the beginning of the leafy stem, so that the phenomenon is only an exhibition of the usual metamorphosis of the foliage-leaves. The difference between the older and younger, *i.e.* lower and upper foliage-leaves, only seems strange because the two kinds of leaf-forms are not usually seen simultaneously on one and the same plant. By the time the crown of a tree has developed, the first (oldest) leaves which adorned the young sapling have long disappeared. Many descriptive Botanists, as a rule, only consider the foliage-leaves of the fully-grown trees and bushes; some of them have hardly ever seen the first leaves of the commonest trees, and when they do happen to come across them they regard them as an extraordinary phenomenon, declare the shoots bearing them to be "bud variations", and draw bold and bewildering hypotheses from their appearance. This alteration in form, however, has nothing to do with the formation of varieties, nor is it dependent either upon the influence of the soil or upon the effect of climate. Moreover, the form of leaf characteristic of the sucker is not possessed by the secondary shoots which arise from the suckers; these are adorned with the same foliage which occurs on the topmost branches of the tree.

Alterations in the scale-leaves as well as in the foliage are brought about by mutilation of the branches. When the upper portions of Willow boughs with their foliage-buds are cut off, leaving the lower portions with the buds of the flower-catkins on them, the small pale scales at the base of the catkins change into green foliage-leaves; the axis bearing these leaves elongates, and the catkins then form the termination of a leafy shoot. Many Willows, *e.g.* *Salix cinerea* and *S. grandifolia*, by this metamorphosis assume a very unusual appearance. In the following year the branches bearing the flower-catkins, if they are

not mutilated afresh, will again put out short catkin-stalks with small pale scales.

Mutilation of herbaceous plants is caused by herbivorous animals, viz. insects and mammals, and on a large scale by man when he mows the meadows and cuts the crops and makes other necessary invasions on the natural vegetation in the interests of husbandry. The alterations caused by these mutilations of the foliage-leaf region are in the main the same as in woody plants. From the remaining stumps of the stem lateral shoots arise whose first leaves are like the first leaves of the seedling. Usually they are less divided and have fewer hairs than the leaves on shoots of normal plants, and on this account they have a very different character. In the floral region the effects of mutilation are twofold—first the peduncles or the lateral axes which are terminated by inflorescences elongate, and then the flowers become smaller. For example, when a vigorous stalk of the Ox-eye Daisy (*Chrysanthemum Leucanthemum*) bearing a capitulum is cut off close to the ground, long lank lateral stems develop from the axils of the lowest remaining leaves, each one ending in a capitulum. The main stem is now seen to be branched at its base, which is never the case in normal plants. If about half the stalk of the common Foxglove is cut off in the spring long flower-racemes will arise from the axils of the leaves just below the cut, but the flowers will be only half as large as those which would have developed on the uncut main stem. The stem of *Althæa pallida* rises a metre above the ground if its development is not hindered, and forms fascicles of short-stalked flowers in the axils of the upper leaves. If the stem is broken off lateral axes develop from the axils of the remaining leaves, and bear little long-stalked flowers. Particularly good examples are furnished by the annual weeds *Delphinium Ajacis*, *Nigella arvensis*, *Stellera Passerina*, and the like, which grow up amongst cereals. Their main stems are broken off when the corn is cut, and they then develop comparatively long branches with small flowers from the remaining stumps. If only single flower-buds, and not the whole inflorescences, are removed from a herbaceous plant whose main stem terminates in a long raceme, so that each flower is cut away in turn from below upwards just before it opens, the rachis of the raceme elongates enormously and flower-buds are developed at its end which would certainly not have unfolded had there been no mutilation. In the Red Foxglove, for example, the rachis of the raceme which has been damaged in this way will grow to twice its ordinary length, and twice as many flowers will be developed. The last and highest flowers in such racemes, however, are only half the size of those which arise on normal racemes.

We must now consider certain perennial meadow plants which when mown down are stimulated by the mutilation to develop flower-stalks in the same year, which would, in the normal course of things, not have flowered till the year following. In Alpine valleys it is a very common thing for the flowers of the spring plants *Anemone vernalis*, *Geranium sylvaticum*, *Gentiana verna*, *Polygonum Bistorta*, *Primula elatior* and *P. farinosa*, *Trollius Europæus*, &c., to appear in

the autumn in meadows which have been mown in the spring. The flowers appearing under these circumstances are remarkable for their small size. Their diameter is at least a third smaller than that of the spring flowers. In conclusion we may refer to the gardener's artifice which has already been described (p. 453) of producing perennial plants with woody stems from an annual Mignonette plant by mutilation. We might also mention the dwarf shrubs and trees produced by combined mutilation and grafting, especially the strange-looking little Ivy trees obtained by grafting a flowering branch of Ivy on an erect stem a span high, and the dwarf Conifers so much in favour with the Japanese.

Gardeners and descriptive Botanists have frequently determined and described mutilated plants as other species, hybrids, or varieties. They are neither the one nor the other. The peculiar appearance of the altered members resulting from mutilation is exactly determined beforehand in each species; it is due to the specific constitution of the species, and thus is part of its being. It is not produced by the external influences which lead to the formation of varieties, but is brought about by inherent necessity quite independent of the influences of climate and soil.

ALTERATION OF FORM BY PARASITIC FUNGI.

A considerable number of the trees and shrubs of Central and Southern Europe bear bristling, much-branched structures on some of their boughs which, from a distance, look like large birds' nests or brooms, and which have been popularly termed "witches' brooms". They are the outward and visible signs of a disease from which the plants in question suffer, and, as their name testifies, their origin was thought to be connected with witches. Traditionally witches have the power of "wishing" harm to mankind, animals, and plants; and superstitious people, at the sight of these peculiar pathological structures on the trees, may have started the idea that the disease was caused by witches that they might have brooms ready at hand for their midnight ride on the Brocken. Other plant diseases have been ascribed to unusual conditions of weather, especially to long-continued rain or great drought. It is not long since the discovery was made that most of the diseases attacking trees, shrubs, and herbs are caused by Fungi, and that atmospheric conditions are only concerned in the matter in so far as they hinder or favour the establishment and development of these parasites.

All the Fungi in question are parasites. They penetrate into the tissues of the host-plant and sooner or later cause the death of the affected part, and frequently of the entire host-plant. The living protoplasm in the cells and tissues of the host which is influenced by the parasite undergoes fundamental changes in its composition. Some of the cells are drained, their living protoplasm being consumed, so to speak, and these cells are obviously marked for destruction. Others are not killed, but changed. The metamorphosis occurs, in the first place, in the constitution of the living protoplasts which have not yet completed their development, the change much resembling that known as fermentation in fluid substances

(*cf.* vol. i. p. 508). In fermentation the chemical composition of the fluid is altered, its chemical compounds are shaken, decomposed, and split up and new compounds are formed by the action of the living Yeast cells. The same thing happens here in the interior of the living plant in its turgid, meristematic tissue—that is to say, in a group of protoplasts which still have the power of growing at the expense of materials supplied them, of increasing in size, and of multiplying by division. But these cells no longer behave as—in the absence of the parasite—they would have done. Profoundly modified under the influence of the parasite, but yet not killed, these cells, by their continued division, form tissues and organs of new and unusual form; in other words, that part of the host which is invaded but not killed by the parasite will continue to grow and increase in size, and in consequence of the change which its protoplasm has experienced will assume a different outward form.

These altered tissue-bodies produced by parasitic Fungi are called *gall-structures*. They are usually characterized by an excessive growth known as hypertrophy, as well as by their altered shape. The hypertrophy is without doubt caused by a stimulus proceeding from the parasite. We may conclude that the significance of the increased growth lies in the abundant supply of nourishment thus placed at the disposal of the parasite, since the large quantity of food-material brought for the excessive development of the hypertrophied growth connotes a large supply for consumption by the parasite. In many cases, however, the hypertrophied tissue merely forms a wall protecting the host against the further depredations of the intruder. It then contains no nourishment for the use of the parasite, being built up chiefly of corky cells, which the latter cannot consume or destroy. Such a tissue might be compared to the so-called callus which grows up in plants in parts deprived of epidermis after an injury, or in other wounds, and gradually covers them over with a protective layer.

The formation of the gall is often restricted to only a *small portion* of the afflicted plant; in other cases *whole leaves* and *branches*, and sometimes even *extensive shoots*, become modified in shape. To get a general idea of the four types of hypertrophied growths it will be best to take them one after the other in the order mentioned, commencing with the simplest.

The simplest of these galls consist of a few degenerate and metamorphosed cells in the centre of an extensive and unaltered tissue. They are produced chiefly by parasites of the genera *Rozella*, *Synchytrium*, *Exobasidium*, and *Gymnosporangium*. *Rozella septigena*, one of the Chytridieæ, develops swarm-spores which attack the various species of the fungal genus *Saprolegnia*. They settle on the tubular branches of the *Saprolegnia* at a place where it was just about to divide and to produce swarm-spores of its own. In consequence of the invasion of the parasite this does not take place, but the tubular cells which would have formed a *Saprolegnia*-sporangium divide instead into short barrel-shaped cells, each of which becomes a sporangium of *Rozella septigena*. In addition to this the infected cells develop lateral outpushings which swell up spherically, and each contains a resting-

spore of the parasite. Parasitic species of *Synchytrium* cause a vesicular enlargement of single cells of the epidermis in the leaves of phanerogamic host-plants. The not uncommon species *Synchytrium Anemones* and *S. Taraxaci* produce only a slight overarching, and the enlargement of the cells is hardly more than four times, often only twice the usual size. But, by the influence of *Synchytrium Myosotidis*, hypertrophied epidermal cells rise up from the leaves of the Forget-me-not (*Myosotis*) in the form of comparatively large, club-shaped, bottle-like, or egg-shaped bladders of golden or reddish yellow colour, and each contains the parasite, or rather its spores. The parts of the leaf attacked by *Synchytrium Myosotidis* are also much thickened, the palisade cells and the air-containing lacunæ of the spongy parenchyma (*cf.* vol. i. p. 279) disappear, and the tissue consists entirely of large similarly-shaped cells which fit close to one another, leaving no spaces between. In the gall caused by *Synchytrium pilificum* on *Potentilla Tormentilla* the much-enlarged cells in which the parasite settles are overgrown by the adjoining hypertrophied cells, some of which rise up in the form of hairs, and the whole new structure resembles a hairy wart.

A curious gall is produced by *Exobasidium Rhododendri* on a sharply-defined portion of the *foliage-leaves* of the Alpine Rose (*Rhododendron hirsutum* and *ferrugineum*). A spherical spongy body rises from a restricted portion of the leaf, usually from the under side of the somewhat projecting midrib, sometimes only as large as a pea, sometimes as big as a cherry, and occasionally even attaining the dimensions of a small apple. It is yellow, but rosy-cheeked like an apple on the side turned to the sunlight, and it reminds one of this fruit by its succulent tissue and sweet taste. Indeed, these galls are sometimes called "Alpine Rose-apples". Their surface is covered with a bloom which is caused by the numerous spores developed there and does not consist of wax like the bloom on an apple rind. The neck joining the gall to the leaf is not more than 1–2 mm. across, and, what is still more remarkable, except for this sharply-defined place of connection the infected leaf is unaltered.

Galls produced by the Gymnosporangia on the leaves of the Mountain Ash, Pear-tree, Rock-medlar, and other Pomeæ exhibit strange forms. One of them, caused by *Gymnosporangium conicum*, on the foliage of the Rock-medlar (*Aronia rotundifolia*), is represented in fig. 357 [2]. It resembles a tubercle furnished with horns projecting from the lower surface of the leaf. Microscopic examination shows that the knob consists of the strangely metamorphosed spongy parenchyma of the leaf. The intercellular spaces which normally contain air are quite filled with the mycelial threads, and in the projecting portion of the tubercle, which is very hard and almost cartilaginous, tubes are inserted which terminate blindly below, where the spores of the parasite are developed, whilst above they are open and fringed, thus allowing the spores to escape. These tubes look like horns to the naked eye. Usually several galls occur together on the same leaf. They are conspicuous at some distance on account of their colour. The chlorophyll is destroyed wherever the mycelium of the parasite extends and a reddish-yellow

colour takes its place, so that orange spots appear on the surface of the foliage, contrasting vividly with the green of the unaltered portions of the leaf.

Galls rising from sharply defined parts of the *stem* are comparatively rare. One of the most remarkable is produced on the stems of a Laurel (*Laurus Canariensis*) by the parasitic *Exobasidium Lauri*. When it appears above the bark it looks like an aërial root, but rapidly grows into a branched spongy body 8–12 cm. long similar in appearance to one of the Fungi belonging to the family Clavarieæ (*cf.* fig. 195[1], p. 21). The galls produced by *Entyloma Aschersonii* and *Magnusii* on the Composites *Helichrysum arenarium* and *Gnaphalium luteo-album*

Fig. 357.—Fungus-galls.

[1] Gall on the stem of the Juniper (*Juniperus communis*) produced by *Gymnosporangium clavariæforme*. [2] Gall on the leaves of *Aronia rotundifolia* produced by *Gymnosporangium conicum*.

take the form of outgrowths, varying from the size of a pea to that of a walnut, developed from special spots on the root. Whether the spherical tubercles growing on the root-fibres of many Leguminosæ, especially those of the Bird's-foot Trefoil (*Lotus corniculatus*), the Fenugreek (*Trigonella fœnum-græcum*), Lady's-Fingers (*Anthyllis Vulneraria*), Lupin (*Lupinus variabilis*), and the Liquorice (*Glycyrrhiza glabra*) are to be regarded as true galls caused by the Bacteria-like organisms invariably to be found in their interior is questionable. According to the most recent investigations they are the outward expression of a case of symbiosis and not of pure parasitism.

Gall developments which involve whole roots or rootlets are found on the Alder (*Alnus glutinosa*), and on the Cabbage (*Brassica oleracea*). The gall which is produced on Alder roots by *Frankia Alni* attains the size of a walnut and has a

curious gnarled appearance; all the fibres of the root-branch thicken in a club-like or tuberous manner and become twisted and entangled with one another. The so-called "Fingers and Toes", caused by the Myxomycete (*Plasmodiophora Brassicæ*), is a gall-like hypertrophy on the root of *Brassica oleracea*, which not uncommonly grows to the size of a man's head.

Many woody plants have galls which alter the internal structure as well as the outward appearance of large tracts of the stem. The parasites settle in the cortical parenchyma, producing hypertrophy there, and afterwards the most varied distortions and alterations in the wood of that region of the stem. The trunk, branch, or twig becomes much swollen or knotted and the cortex rent and torn. Resin or a gummy mucilage sometimes runs out of the rifts in the gall. As such a parasite exercises its metamorphosing faculty for several years, the canker (as it may be termed) increases in size continually. Sporangia of varied form and colour appear annually on the affected places, and again disappear when they have shed their spores. The part of the stem or branch above the cankerous cushion dwindles and dies off sooner or later. It rarely happens that the tree or shrub is able to rid itself of the parasite. Occasionally a growth of wood and cork from the adjoining healthy part walls in the cankerous spot so that the parasite is destroyed. The gall produced by *Gymnosporangium clavariæforme* on the trunks and branches of the common Juniper (*Juniperus communis*) is an example of this form (see fig. 357[1]). From the hypertrophy there project in the early spring golden-yellow tongues (shown in the figure) consisting of masses of spores embedded in mucilage. Other similar growths are produced on species of Juniper by *Gymnosporangium conicum*, *G. Sabinæ*, and *G. tremelloides*, but it would take too long to describe their differences in detail. It is important to mention, however, that each of these parasites has two stages of development, living on different hosts, the hypertrophies as well as the associated spore-producing organs of the parasite being different in the two cases. The "Æcidium stage" produces cartilaginous swellings (see p. 520) in definite spots on the foliage of various Pomeæ (*Aronia*, *Cratægus*, *Pyrus*, *Sorbus*), the "Teleutospore stage" thickenings and tuberous outgrowths on the trunks of Junipers (*Juniperus communis*, *excelsa*, *Sabina*), and these parasites can travel from one host to the other in turn. (The two stages on different hosts are shown in fig. 357; these are not of the same fungus, but of nearly allied ones, and illustrate the point mentioned.)

The parasite *Peziza Willkommii* attacks the trunks and branches of the Larch (*Larix Europæa*), and produces the well-known Larch-disease or "Larch-canker". The parasite having gained access at some point on the stem or branch first penetrates the cortical parenchyma, and affects the cambium so as to prevent the further development of wood in that place. The development of the wood on the opposite side of the stem, *i.e.* the formation of annual rings, may proceed for several years, and in this way the attacked spot on the trunk takes the form of a depression, which is rendered the more conspicuous should the wood and cortex surrounding the parasite have undergone a greater thickening than usual. In

time the patch becomes a sunken, blistered hole from which resin flows; and every year the fructifications appear above the cortex in the form of numerous little cup-like structures which are white outside and scarlet-red in the concavity. As the disease progresses the infected patch gradually spreads, and infected trunks and branches can be easily distinguished at a distance. Towards the end of summer the needles on the twigs above the canker turn yellow, while those on the healthy branches are still a beautiful green. This premature discoloration is a sure sign of the speedy death of the whole bough. A similar canker is produced on the

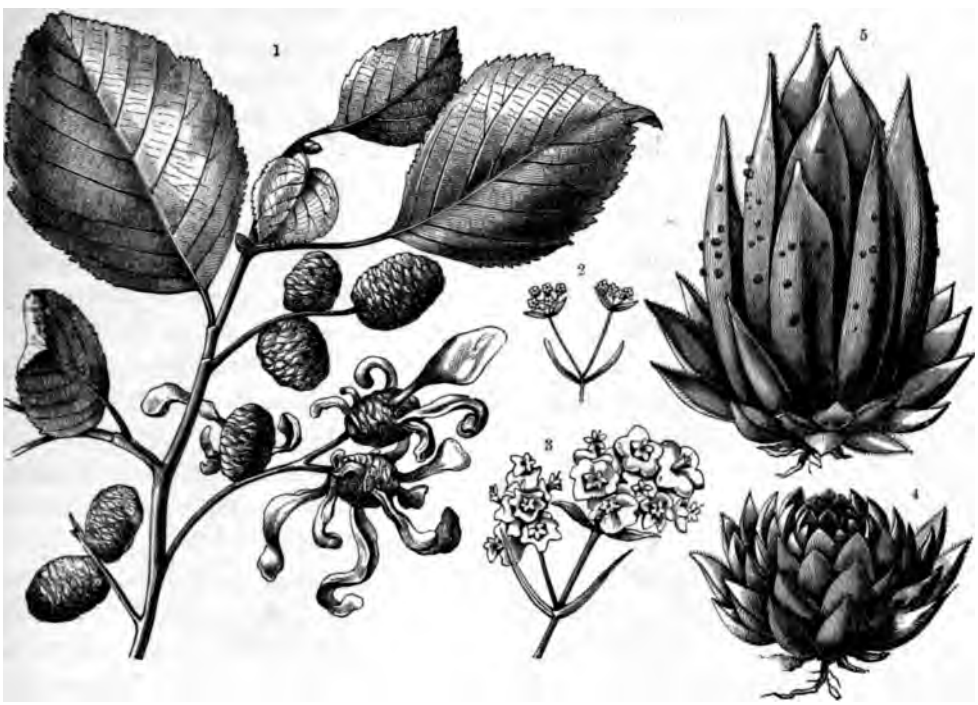

Fig. 358.—Various Galls.

[1] Gall on the bract-scales of the pistillate flowers of the Gray Alder (*Alnus incana*) produced by *Exoascus Alni-incanæ*. [2] Inflorescence of *Valerianella carinata*. [3] The same inflorescence with galls produced by a gall-mite. [4] Leaf rosette of the House-leek (*Sempervivum hirtum*). [5] Leaf rosette of the same plant which has been attacked by the fungus *Endophyllum Sempervivi* and has become hypertrophied.

Silver Fir (*Abies pectinata*) by *Æcidium elatinum*, but instead of being only on one side of the branch, as in the Larch, it forms a uniform swelling all round it. Cankers of this kind are produced by a Bacterial organism (*Bacillus amylovorus*) on fruit-trees (Apple, Pear, &c.), and on various trees belonging to the Amentiferæ (Beeches, Hornbeams, Oaks, &c.) by the Fungus *Nectria ditissima*.

When *whole leaves* undergo hypertrophy of the kind we have particularly remarkable changes of form. For example, the normal leaves forming the rosettes of the House-leek (*Sempervivum hirtum*; see fig. 358 [4]) are broadly obovate in form, being little more than twice as long as they are broad. The leaves of the same plant after they have been attacked by the parasitic *Endophyllum Semper-*

vivi (see fig. 358 [5]) are seven times as long as broad and linear in shape. They stand erect, and are of a much paler colour than the healthy leaves. The Wood Anemone (*Anemone nemorosa*) affords another example (see fig. 259, p. 229). It spreads by creeping stems under the surface of the ground, and forms small colonies in light thickets and in meadows. The plants consist partly of flowering lateral shoots, and partly of foliage-leaves, which emerge above the ground from the creeping underground stem. In normal leaves the erect petioles are all the same length, and the leaflets are extended at about the same level. But when the *Æcidium* stage of *Puccinia fusca* has settled on them this becomes altered. The blades of the infected leaves tower over their healthy neighbours in consequence of the elongation of their petioles, whilst their leaflets are smaller and less divided. The length of the petiole in normal leaves is some 12–13 cm., in hypertrophied leaves 15–18 cm.; but the size of the altered segments, compared with those of normal leaves, is as 5 : 7. Similar changes are observed in leaves of *Soldanella alpina* when attacked by *Puccinia Soldanellæ*. The petioles of the infected leaves are 2–4 times as long as the normal ones, the blade is smaller and hollowed like a spoon instead of being flat, and the colour is an ochreous yellow instead of a dark green. The same alterations in the length of the petiole, and in the size and colouring of the leaf-lamina, are produced in the leaves of *Alchemilla vulgaris* by *Uromyces Alchemillæ* and in those of *Phyteuma orbiculare* by *Uromyces Phyteumatum*. To this class belongs also the so-called "curl" disease of Peach and Almond trees, produced by *Exoascus deformans*, and rendered conspicuous by the considerable enlargement, undulation, and bladder-like expansion of the infected leaf-surface, which acquires generally a very brilliant coloration.

Floral-leaves are comparatively seldom metamorphosed by Fungal parasites. In the Alder (*Alnus glutinosa* and *incana*) the bracts of the pistillate flowers are changed by *Exoascus Alni-incanæ* (=*E. amentorum*) into elongated purple-red spatulate lobes much twisted and bent (see fig. 358 [1]); *Peronospora violacea* sometimes causes the stamens to change into petal-like structures in the flowers of *Knautia arvensis*, so that they then seem to be "double"; *Ustilago Maydis* causes a growth of tissue in the pistillate flowers of the Maize, the result being that instead of grains irregular cushion-like structures 7 cm. in diameter are produced. *Taphrina aurea*, which settles on the pistillate flowers of Poplar (*Populus alba* and *tremula*) causes the ovaries to form golden-yellow capsules more than twice the usual size. The galls produced by *Exoascus Pruni* on the ovaries of wild Plum, Bullace, Sloe, and Bird Cherry (*Prunus domestica, insititia, spinosa, Padus*) belong also to this class. The tissue of the ovary increases in size, but not in the same way as in fruit formation. The resulting body is flattened on two sides, brittle and yellow; the seed inside is abortive, and a hollow space is left in its stead. The gall produced from the ovary of *Prunus domestica* has the form of a rather curved pocket, which looks as if it had been powdered outside with flour at the time the spores ripen. These hypertrophies, which are popularly termed "pocket-plums", "bladder-plums",

&c., fall off the trees at the end of May. They are eaten in many districts, but have an insipid, sweetish taste.

Galls consisting of *whole shoots*, both the stem and its leaves being altered by the parasite, are found principally on trees and shrubs, and only rarely on herbaceous plants. Examples of the latter, however, are furnished by the metamorphosed shoots of the Shepherd's Purse (*Capsella Bursa-pastoris*) produced by *Cystopus candidus* and *Peronospora parasitica*. Here the leaves, especially the floral-leaves, as well as the ground-tissue of the stem undergo pronounced hypertrophy. The petals, which measure only 2 mm. in length in a healthy plant, may become even 15 mm. long; the sepals also elongate, become fleshy and brittle, and are distorted and crumpled in all manner of ways. Only six stamens are developed in normal flowers, but in hypertrophied specimens there are often eight. The metamorphosis produced by *Uromyces Pisi* in one of the Spurges, *Euphorbia Cyparissias*, is even more remarkable. The stem elongates far beyond its usual dimensions, and the leaves, which are crowded together on normal shoots, are thus separated by considerable intervals. The distance between two adjoining successive leaves in the healthy *Euphorbia Cyparissias* is only 0·5 mm., but in the hypertrophied specimens it becomes 2–3 mm. Infected shoots on an average are twice as high as healthy ones. The foliage-leaves, which are thin, flexible, linear, and twelve times as long as they are broad in the healthy plant, become, in the infected specimens, thick, brittle, elliptical, and only 2–3 times as long as they are broad. The bluish-green colour of the normal plant is changed into a yellow-ochre tint, and this contributes not a little to the odd appearance of the plant. Affected plants are not uncommon in Switzerland; a locality in which this disease has been very prevalent in recent years being Saas-Fée in the Saas-thal. The metamorphoses produced on the shoots of Periwinkles (*Vinca herbacea*, *major*, and *minor*) by the Uredospore-stage of *Puccinia Vincæ* and on shoots of *Cirsium arvense* by the Teleutospore-stage of *Puccinia suaveolens* are very like those of the *Euphorbia* just mentioned, since the stem becomes much elongated and the leaves shorter, broader, yellow, and brittle. When flowers are developed on these affected shoots, they are more or less abortive and sickly, and no fruits or fertile seeds arise therefrom. Frequently the shoots blossom prematurely. For example, we can at once detect by its elongated rosette-leaves when *Primula Clusiana* and *minima* are infected by *Uromyces Primulæ integrifoliæ*, and it may be observed when this is the case that the shoots do not wait until the next spring to develop the flowers laid down in the summer, as usual, but open them in the autumn of the same year instead.

The Cowberry (*Vaccinium Vitis-Idæa*) is especially worthy of notice among low woody plants, because two kinds of parasite attack its shoots. *Melampsora Gœppertiana*, in the Teleutospore-stage, causes a marked, gouty thickening in the cortical parenchyma, which is converted into a spongy tissue; at first it is flesh-coloured, but soon assumes a chestnut-brown tint. The stems elongate very much and grow vertically upwards; and when several of them close together are thus attacked they present a besom-like appearance. The foliage-leaves are much

farther apart than in the healthy plant on account of this stretching of the stem. The lower leaves of the shoot are transformed into small fringed scales, and the upper ones are so much shortened that their outline becomes almost circular. The second parasite to which the Cowberry shoot is subject is *Exobasidium Vaccinii* (a near ally of the already mentioned *Exobasidium Lauri*, p. 521). The stem becomes pale rose-red colour, and rather thickened and spongy, but it does not elongate much more than usual; the leaves become blistered and curiously convex on the

Fig. 359.—A Witches' Broom on the Silver Fir, produced by *Æcidium elatinum*.

under surface. The substance of the infected leaves becomes brittle and loses its chlorophyll. A red tint appears in place of the green, especially on the upper surface of the leaf, whilst the lower surface, on which the spores develop, looks as if it had been dusted over with flour. Usually the buds develop prematurely on these shoots, *i.e.* the buds which, under ordinary circumstances, would not develop until the next year push out and form new shoots shortly after they have been laid down. The axes of these shoots, however, remain short; their leaves are closely crowded, red in colour, and sessile. From a distance the premature shoots look like large double red flowers inserted in the dark green of the non-infected Cowberry bush. The shoots which develop prematurely on the shrubs of the Bog Whortleberry (*Vaccinium uliginosum*) by the action of *Exobasidium Vaccinii* are often met with in alpine regions, and are even more noticeable on account of their fiery-red

colour. The Bearberry (*Arctostaphylos Uva-ursi*), *Ledum palustre*, and the Marsh Andromeda (*Andromeda polifolia*) are subject to similar metamorphoses at the hands of *Exobasidium Vaccinii*, so that *Vaccinium Vitis-Idæa* may be regarded as typical of them.

When the shoots of the larger shrubs or trees are metamorphosed by parasitic Fungi attacking their branches, we have the formation of the structures popularly termed Witches' brooms, which were mentioned at the beginning of this chapter. The stimulus necessary for their formation is afforded in different plants by different parasites; on Barberry bushes (*Berberis vulgaris*) by *Æcidium Magelhænicum* (to be distinguished from the common *Æ. berberidis*), on the Gray Alder (*Alnus incana*) by *Exoascus epiphyllus*, on the Hornbeam (*Carpinus Betulus*) by *Exoascus Carpini*, on the Bullace (*Prunus insititia*) by *Exoascus insititiæ*, on other species of the genus *Prunus* by *Exoascus Cerasi*, on the Birch (*Betula verrucosa*) by *Exoascus turgidus*, on the Weymouth Pine (*Pinus Strobus*) by *Peridermium Strobi*, and on the Silver Fir (*Abies pectinata*) by *Æcidium elatinum*. Witches' brooms also occur on the Mastic tree (*Pistacia Lentiscus*), and on Beeches, Pines, Larches, Spruce Firs, &c., although hitherto we have not been able to ascertain definitely what parasitic Fungi are the cause in these cases. The Witches' broom of the Silver Fir has been selected and figured (see fig. 359) as a type of these peculiar structures. It always grows on one of the horizontally projecting lateral branches of the Fir, and raises its erect or curved twigs from the upper side, resembling, as it were, an epiphyte growing on the bark of the horizontal bough. The twigs are grouped in whorls and not in two rows, as usually happens in the lateral shoots of the Silver Fir. They are all shortened and thickened, and remarkably soft and pliable, because the cortical parenchyma has become spongy and the wood is only slightly developed. The buds, which in healthy tissue are egg-shaped, are almost spherical here. As in other instances of hypertrophied plant-members, we have a precocious development, a so-called "prolepsis", in these Witches' brooms. The buds swell earlier and unfold earlier than those of healthy twigs. The leaves remain short, yellow, somewhat crumpled, and fall off when a year old, while those of normal twigs are long, linear, straight, dark green on the upper side, and remain in position from 6–8 years. The growth of the twig is restricted; it dies off in a few years, and then, inserted on the dark green branches of the Silver Fir, remain the dry, bristling brooms, whose appearance has stimulated the imagination of the peasantry and given rise to the superstitions alluded to at the beginning of this chapter.

ALTERATION OF FORM BY GALL-PRODUCING INSECTS.

Certain members of the Arachnoidea, Diptera, and Hymenoptera, which attack and penetrate the tissues of living plants and incite the formation of peculiar excrescences, are known as gall-mites, gall-gnats, and gall-wasps. The

growths, like small rosy-cheeked apples, which occur on the foliage of Oaks, popularly known as "oak-apples", are amongst the best known. The terms "gall" and "gall-apple" were used by writers in the sixteenth century, and (like the Old English word *galle*, the French *galle*, and the Italian *galla*) are derived from the Latin word *galla*, used for these outgrowths by Pliny in his Natural History. The sixteenth-century writers distinguish between "gall-nuts" and "gall-apples", meaning by the former the small hard outgrowths on the leaves of Beech-trees. Afterwards the word *gall* was used for all the outgrowths produced by animals on green living plants. More than that—the hypertrophies described in the preceding chapter, produced in green host-plants by the various families of Fungi, are also included under the term. It has been proposed recently to substitute the word *cecidium* for *gall*, and to distinguish the excrescences as myco-cecidia, nemato-cecidia, phyto-cecidia, diptero-cecidia, &c., according as they owe their origin to Fungi, Thread-worms (Nematodes), Gall-mites (*Phytoptus*), Gnats (*Diptera*), &c. A systematic classification of this sort, on the lines of the classification of animals, might be of use to Zoologists, but to the Botanist its value is only secondary. He must, as in other similar cases, keep to morphology as the primary ground of classification, and has to arrange the structures according to their agreement in development. Moreover, in a general review, it is necessary to consider whether a whole group of plant-organs or one alone undergoes metamorphosis; and the starting-point of the outgrowth must also be ascertained; *i.e.* whether it is the foliage-leaves, floral-leaves, stems, or root-structures, &c., which are the head-quarters of the excrescence.

When the gall originating as the nest or temporary habitation of a single animal or colony of animals is limited to a single plant organ it is said to be *simple*; if, on the other hand, several plant organs are concerned in its production it is said to be *compound*.

Simple galls may, for convenience of description, be divided into (1) *Felt-galls*, (2) *Mantle-galls*, and (3) *Solid galls*. The Felt-galls are chiefly due to hypertrophied epidermal cells growing out into hairy coverings of various sorts and shapes; Mantle and Solid galls, however, are rather more complicated. In both cases insects are present in swellings of various descriptions, but there is this essential distinction: — The Mantle-gall is a hollow structure which, though it may arise in various ways and assume a multiplicity of forms, always has a portion of the surface of the affected organ for its lining—in other words, it is a chamber formed by hypertrophied growth *around* the place occupied by the insect. In the Solid gall, on the other hand, some spot is *pierced* by an insect and the eggs deposited *in* the tissues (not on the surface), the punctured spot forms a swelling with the larva inside, but the lining of the chamber is in no sense a portion or development of the original surface of the organ affected. Again, whilst in most mantle-galls the cavity of the gall is in open communication with the outside, and the insect can escape by this aperture (though this is not invariably the case), in the solid gall there is not such opening, and the insect

has to bore its way out. Needless to say, of both these types there are numerous modifications, but they fall into the two classes (of mantle and solid galls) according to their mode of development.

The majority of *felt-galls* are produced by gall-mites. They form cottony or felted growths on limited and sharply defined areas of green leaves and stems, the surface of which is otherwise smooth, or possesses but few hairs. Sometimes they have the form of small tufts, bands, or stripes, sometimes of large spots with irregular contour. In most instances the felt is situated on the under side of the foliage-leaf, and the gall-mite usually prefers the projecting veins to the green surface. In the Lime, Alder, Hornbeam, and Horse-Chestnut, the mites usually establish themselves in the angles formed by the lateral strands where they arise from the midrib, the projecting veins forming the framework for the felted hairs. In the Bramble (*Rubus*) and the Burnet (*Poterium*) it sometimes happens that the felt is continued down from the lamina to the leaf-stalk, and occasionally the green cortex of the succulent twig is covered with felted bands and spots. In some Brambles and Cinquefoils the sepals become furred by the action of gall-mites, the usual consequence being that the outline also becomes distorted. A swelling or slight hollowing of the green leaf-tissue very frequently accompanies the formation of felted galls, in which case the hairy covering is only visible on the concave side whilst the other remains smooth. This is most remarkable in the foliage of the Avens (*Geum*), Vine (*Vitis*), and Walnut-tree (*Juglans*), where a dozen white or brown-felted pit-like depressions are sometimes to be seen on the under side of a single leaf. The colour of the felted hairs is white in the leaves of Beeches, Limes, Bird Cherry, Brambles, Cinquefoils and Burnets, green in the common Maple, yellow in the Spindle-tree (*Euonymus verrucosus*), sulphur-yellow in *Alnus orientalis* and Black Poplar (*Populus nigra*), carmine red at first and then violet in *Alnus viridis* and in the Birches (*Betula alba, carpatica*, &c.), and brown in the Avens (*Geum macrophyllum*), Horse-Chestnut (*Æsculus Hippocastanum*), and in the Aspen (*Populus tremula*). The felted galls which are light in their young stages usually take on a brown tint afterwards. Microscopic investigation has shown that in the formation of felted galls, the epidermal cells, originally tabular in shape and closely fitting, swell out and become transformed into bent and twisted tubes generally shaped like a club or retort, the stimulus being afforded by a minute gall-mite (*Phytoptus*). These cells look like short hairs to the naked eye, and as they stand side by side in large numbers the covering has a velvety or felted appearance. The mites which produce the felt, deposit their eggs in the juicy hair-shaped cells, and their young live on the materials contained in them. It should be mentioned that formerly these velvety and felted coverings were regarded as Fungi, and were described as distinct genera under the names *Erineum* and *Phyllerium* (*e.g.* the gall known as *Erineum quercinum* on the leaves of *Quercus Cerris*). To this group belongs also the gall occurring on the Wood Meadow Grass (*Poa nemoralis*) consisting of cells which resemble root-hairs, which is produced by the gnat *Hormo-*

myia Poæ. The hair-shaped cells are epidermal, and spring from the stem above the nodes; they break through the leaf-sheath which proceeds from the adjacent node, and are arranged in two groups, which grow in opposite directions, so as to wrap round the stem from the two sides. The whole hairy mass looks as if it had been parted into two. At first the hairs are white; later they become light brown, and when the gall is fully developed they have the form of brown felted strands, wound round the stems and firmly inclosing the larva of the gnat in question.

A large number of simple galls are grouped together under the name of *Mantle-galls*. The insects which give rise to them spend their lives on the surface of the leaves, where they multiply and attach their eggs to the epidermis. A growth is excited in certain layers of the cell-tissue by the stimulus which the animals exercise on their place of settlement. Cavities are thus formed which serve as dwellings for the animals and their brood, and which surround them like a protecting mantle. Mantle-galls may be divided according to their structure into *scroll-*, *pocket-*, and *covering-galls*. *Scroll-galls* are caused by gall-mites, leaf-lice, tree-hoppers, and flies, and usually occur on the blades, rarely on the petioles of the leaves. The surface inhabited by these animals, which, in the ordinary course of things would have spread out flatly, grows more luxuriantly on one side than on the other, and the result is the formation of a scroll, *i.e.* of a chamber in which the animals are hidden. It is always the side on which the animals live which becomes concave, and the leaf is usually curled up lengthwise. In the Alpine Rose (*Rhododendron*), Crane's-bill (*Geranium sanguineum*), and Orache (*Atriplex hastata, oblongifolia*, &c.), it is the upper side of the leaf which is tenanted by the insects, and is therefore the one to roll up; it is the lower side, however, in the Buckthorn (*Rhamnus cathartica*) and the non-climbing species of Honeysuckle (*Lonicera alpigena*, &c.). In many instances the whole leaf-lamina is rolled up, but more frequently the alteration is restricted to the edge of the leaf when the margin appears to be bordered with a swollen hollow cushion often corrugated or undulating. In the Alpine Rose (*Rhododendron ferrugineum* and *hirsutum*) both halves of the leaf-blade are rolled round (see figs. 360 [2] and 360 [3]), but usually the rolling is so slight that the gall has the form of a boat or hollow trough. Sometimes an alteration in the shape of the leaf accompanies the rolling. For example, the foliage of the Abele (*Populus alba*) on which *Pachypappa vesicalis* establishes itself when the leaves are very young, exhibits in addition to the rolling a deep hollowing of the blade. Instead of the short blunt lobes, long pointed segments are formed, which stand side by side when they are rolled up, and cross over one another in many ways so that the mantle-gall on the hollow side is shut in by a veritable lattice-work. The parts of the tissue brought into contact by the rolling do not fuse together, and therefore the cavity in which the gall-producing insects live is always in open communication with the exterior. In most cases the tissues concerned are thickened, brittle, more or less devoid of chlorophyll, and yellow in colour. Not infrequently a red pigment is formed in them, so that the outside of the gall has a yellowish-red colour. The scroll-gall produced by the hemipterous

Trioza Rhamni on the margin of Buckthorn (*Rhamnus cathartica*) leaves is very hard and thickened like cartilage. In many plants the epidermal cells lining the gall elongate into hairy structures, as in the felt-galls previously described. Their juicy contents are used as food by the young gall-mites. This is the case, for example, in the Alpine Rose (*Rhododendron ferrugineum, cf.* fig. 360[3]). ***Pocket-galls*** are closely allied to the scroll-like forms. The tissue of the leaf-lamina or

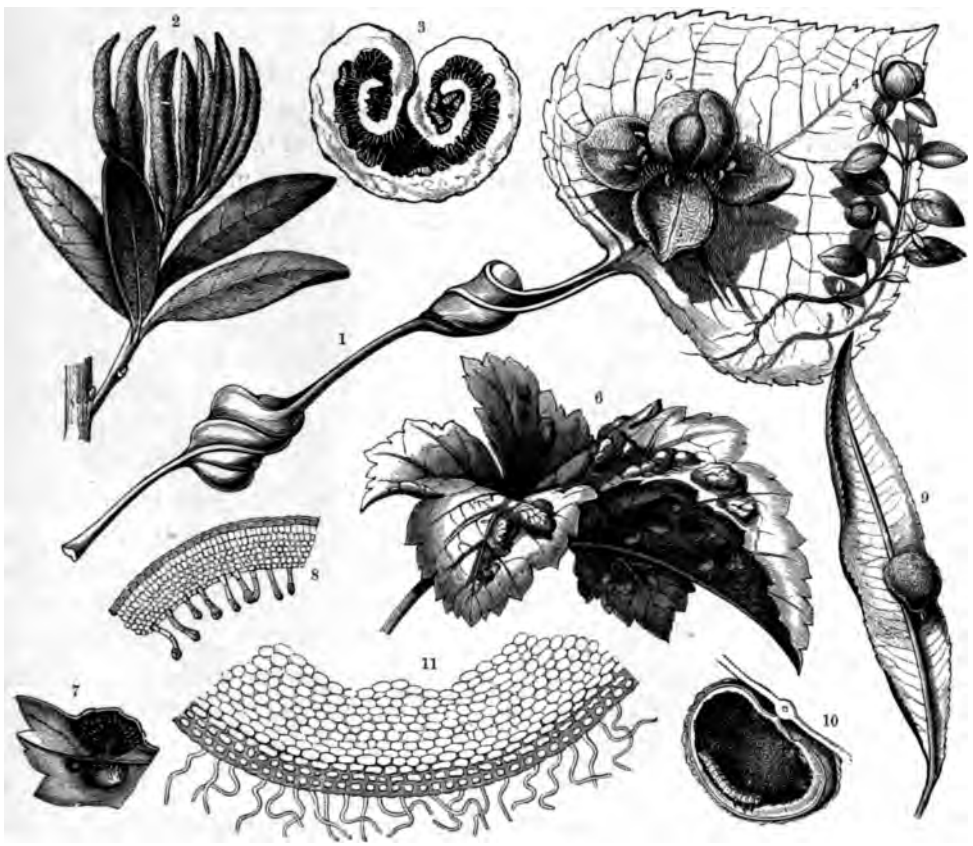

Fig. 360.—Galls.

[1] Covering-galls on the petiole of the Black Poplar (*Populus nigra*) produced by *Pemphigus spirotheca*. [2] Scroll-galls on the leaves of an Alpine Rose (*Rhododendron ferrugineum*) produced by gall-mites. [3] Transverse section of one of these galls. [4] and [5] Bud-galls on the branchlets of the Wild Thyme (*Thymus Serpyllum*) produced by gall-mites. [6] Blister-like galls on the leaf of the Red Currant (*Ribes rubrum*) produced by *Myzus ribis*. [7] Part of the leaf seen from below. [8] Vertical section of a portion of this gall. [9] Solid gall on the leaf of the Gray Willow (*Salix incana*) produced by *Nematus pedunculi*. [10] The same gall cut open. [11] Part of the wall of this gall in vertical section. [1], [2], [4], [6], and [9] natural size; [3] and [6] × 4; [5] and [7] × 8; [8] and [11] × 50.

petiole and sometimes that of the cortex in young twigs is subjected to a stimulus where the animals (gall-mites, leaf-lice, diptera) settle, with the result that a hollow protuberance arises whose excavated cavity serves as a temporary dwelling for the insects. The protuberances exhibit a great variety of form and shape, and they differ considerably in their internal structure. The following are the most noticeable forms. First, the plaited galls. They form deep, plaited, sometimes twisted channels in the leaf-tissue which open on the upper side by a narrow hole. and

project like weals on the lower surface of the leaf. The growing tissue which forms the floor of the channel is yellow and often lined with short hairs. The channel usually follows the course of the larger veins of the lamina, and sometimes actually traverses one. Plaited galls are produced by gall-mites. The best known are those on the foliage of *Carpinus Betulus*, *Clematis Flammula* and *C. recta*, and *Ribes alpinum*. Wrinkled galls come next to the plaited form. The protuberance is here limited to the green tissue shut in by strong rib-like projecting veins, and is only shallow; the upper side of the leaf has bulgings and protuberances and the lower pits and cavities. The protuberances are always developed in numbers close together, so that the leaf looks very much wrinkled in that region. Examples of this form are furnished by the wrinkled galls on the Elm (*Ulmus campestris*; see fig. 361 [4]) produced by the leaf-louse *Schizoneura Ulmi*, and on the Red Currant (*Ribes rubrum*; see figs. 360 [6, 7, 8]) by another leaf-louse, *Myzus ribis*. In the latter several wrinkles are usually united into large blister-like protuberances, red on the outside, and covered with jointed cellular structures bearing glands which look to the naked eye like short hairs. This form, though resembling certain felted galls, is distinguished from them by the different form of the hairs arising in consequence of the stimulation. In the Mouse-ear Hawkweed (*Hieracium Pilosella*) leaf-fleas (*Psyllodes*) produce minute protuberances with narrow mouths, which stand out from the lower side turned towards the ground like small warts, and when they occur close together give a corrugated appearance to the leaf. Hollow protuberances of this sort arising upon restricted areas of the leaf-surface, and growing very actively, give rise to bag or sack-like structures attached by a very narrow neck. From their resemblance to a head such galls are sometimes termed capitate galls (*Cephalonion*). In others, where the outgrowth is fairly thick-walled and in form horn-like, the designation horn gall (*Ceratonion*) has been given. Between these forms numerous intermediate forms exist which may be compared to pockets, bags, nails, &c. Many of these galls project from both the upper and lower side of the leaf, as though a nail had been driven through it—hence the last-mentioned name. The capitate-gall of the Sloe (*Prunus spinosa*), caused by a gall-mite, projects almost as much from the under as from the upper side, whilst the similar gall on the foliage of the Bird Cherry (*Prunus Padus*) rises on the upper side as a long pocket, but below only projects like a small wart. Many capitate and horn-like galls are developed only on one side, and here again there is a very great variety. When the protuberances are due to mites the cavity always opens on the lower side of the leaf. Both the inner wall and mouth of the cavity are covered with hairs, and sometimes the aperture seems to be actually plugged up by them. In the bag-shaped protuberances produced by the leaf-louse *Tetraneura Ulmi* on Elm leaves, a relatively large slit is formed just at the narrow part of the bag at the moment when the insects leave the cavity (see fig. 361 [5]). The external surface of the protuberances caused by mites on the foliage of Alders (*Alnus*), Maples (*Acer*), and Limes (*Tilia*) is smooth, in those of the Bird Cherry (*Prunus Padus*),

and Wayfaring Tree (*Viburnum Lantana*) ciliated, whilst in the inflated galls of the Elm caused by the white woolly leaf-louse (*Schizoneura lanuginosa*), it is covered with fine hairs like velvet. The capitate galls on the foliage of Maples, Alders, and Limes, of the Guelder-rose and Strawberry, are scattered abundantly over the whole lamina; in the Sloe they stand out chiefly from the margin of the leaf, and in Elms they occur singly or in groups on its central portions. The size of these galls depends upon their distribution. Those which rise in hundreds from the

Fig. 361.—Galls.

1–2 Solid galls on a Rose-leaf; 1 of *Rhodites Rosæ*, 2 of *Rhodites Eglanteriæ*, 3 of *Rhodites spinosissimæ*. 4 Wrinkled galls on an Elm-leaf (*Ulmus campestris*) produced by *Schizoneura Ulmi*. 5 Purse galls on the same leaf, produced by *Tetraneura Ulmi*. 6 Covering gall on the same leaf, produced by *Tetraneura alba*. 7 Solid galls on the leaf of the Purple Willow (*Salix purpurea*), produced by *Nematus gallarum*. 8 Solid galls on the leaves of the same Willow, produced by *Nematus vesicator*.

same lamina have a diameter of 1–3 mm., while those which occur singly or in small groups, often attain a diameter of 2–3 cm.

Contrasting with these embossed or *pocket-galls* are the *covering galls*, forming a third type of mantle-gall. In these, as in the embossed forms, the insects producing the galls live in their cavities, but the course of development is quite different in the two cases. The tissue round the place where an animal has settled or where an egg has been fastened to the epidermis in this type begins to grow, rising up in the form of a fleshy mound or wall which continues to grow until the animal is wholly roofed in. The cavity in this case does not arise from an excavation (as in the embossed or "pocket" type), but from an overarching of the tissue. The

external appearance of these galls is very varied. One of the simplest forms occurs on the leaves of the Ash (*Fraxinus excelsior*, see fig. 362[3]), where it is produced by the gall-gnat *Diplosis botularia*. The insect having laid its eggs in the channelled depressions above the leaf-veins, fleshy cushions arise on either side of the groove which meet above and roof them over. The cushions of tissue forming the roof do not fuse; their succulent edges merely meet, and when the time comes for the gall-gnats to leave their temporary abode the tissue dries up and shrivels,

Fig. 362.—Galls.

[1] Pine-apple gall on twigs of the Spruce Fir produced by the Spruce-gall Aphis (*Chermes abietis*). [2] Covering gall on the petiole of the pyramidal Poplar (*Populus pyramidalis*) produced by *Pemphigus bursarius*. [3] Covering galls on an Ash leaf (*Fraxinus excelsior*) produced by *Diplosis botularia*. [4] Covering gall on Pistacia (*Pistacia Lentiscus*) produced by *Pemphigus cornicularius*. [5] Solid galls on the cortex of *Duvaua longifolia* produced by *Cecidoses Eremita*. [6] Longitudinal section of one these galls. [7] Capsule galls on the leaf of the Turkey Oak (*Quercus Cerris*) produced by *Cecidomyia serrulæ*. [8] One of these galls cut through with the operculum still firmly attached, and [9] the same with the operculum falling away; × 3. The remaining figures natural size.

leaving a gaping slit as shown in fig. 362[3]. The same thing happens on the leaves or rather leaf-veins of the Stinging-nettle (*Urtica dioica*) and of the Alder (*Alnus glutinosa*), where the galls are produced by gall-gnats (*Cecidomyia urticæ, alni*), and on the midrib of Elm leaves (*Ulmus campestris*; see fig. 361[6]), where the galls are produced by a leaf-louse (*Tetraneura alba*).

The so-called turpentine gall-apples (*Carobe di Giude*; see fig. 362[4]), which

are caused by leaf-lice on various species of *Pistacia*, also belong to the covering class. The rudiment of a foliage-leaf, which in the normal course of events would have developed into a pinnate leaf with dark-green elliptical leaflets, grows out into a pod-like structure not unlike a locust-bean (fruit of *Ceratonia Siliqua*). These galls are longitudinally grooved, and it can be seen more or less distinctly that the furrows correspond to the edges of the leaflets, only here the leaflets have become wrapped in, very much thickened and elongated, and fused with one another. In the cavity inclosed by the fused leaflets lives a colony of leaf-lice (*Pemphigus cornicularius*) which have developed under the protection of the gall. When it is time for them to leave the cavity the top of the pod opens by the separation and bending back of the tips of the fused leaflets which form the wall of the cavity (see fig. 362[4]). The Chinese galls of commerce, produced also by Aphides (on *Rhus semialata*), develop much in the same way. They are hollow, irregularly pear-shaped structures with thin walls covered externally with a gray down. Two other covering galls which deserve special mention on account of their form arise on the petioles of the Poplar, particularly on the species *Populus nigra*, *pyramidalis*, and *dilatata*. The one, caused by a leaf-louse, *Pemphigus bursarius* (see fig. 362[2]), consists of a smooth expansion, red in colour externally, on the upper side of the grooved petiole. If the local swelling be cut through it is seen to be hollow, the cavity in which the leaf-lice live being shut in by thick fleshy walls. The fleshy tissue of the walls is formed by a growth of the cells round the place where the gall-producing insect has settled. A hole is formed at a point remote from the petiole (where the growing tissue met and formed a dome) as soon as the time comes for the inhabitants to make their exit. This is bordered by thick lips as shown in fig. 362[2]. The other gall which appears on Poplar petioles, produced by *Pemphigus spirotheca*, is formed by the thickening of the edges of the grooved petiole, which rise up as fleshy cushions and meet above the depression. At the same time the petiole undergoes a spiral twisting, and a gall is thus produced whose cavity is spirally twisted like the interior of a snail's shell. The thickened edges of the petiole do not fuse; at first they fit close to one another, but later on they separate, and a spiral hole out of which the white, downy leaf-louse can creep is the result (see fig. 360[1], p. 531).

We will now leave the mantle-galls and pass on to a consideration of the *solid* or *tubercular galls*. These are of the nature of swellings of limited size on single plant-organs, and are produced by insects which *pierce the plant-tissue and lay their eggs in the wound*. In this way either the epidermis of the chosen spot alone is injured, or the egg is inserted into the deeper-lying tissues. In both cases an active cell-division is incited in the neighbourhood of the injury. If, however, the egg has only been deposited in the epidermis, the larva which arises from it must penetrate into the interior of the now swollen tissue; when the egg is laid at once deep down this farther penetration on the part of the larva is of course unnecessary. The cavity in which the larvæ dwell may be called the larval chamber, and this sort of gall can be classified according to the number of chambers which it contains,

whether only one or several (*cf.* figs. 363[2] and 363[7]). A great variety is met with in the structure of the wall of the larval chamber. It always has a layer of juicy, thin-walled cells immediately surrounding the egg, known as the medulla or pith of the gall, and an outer layer which surrounds the inner like a skin or bark (see fig. 360[10]). In most instances a third layer is inserted between them which consists of very hard cells forming a protective layer. It should also be noted that the layers of the wall of the gall separate in many instances, so that it is possible to distinguish an "inner" and an "outer gall". The gall-pith furnishes the larva with food when it emerges from the egg, and for this purpose the cells are stored with nourishing substances. The development of the pith takes place with great rapidity, and begins as soon as the egg has been laid in the tissue. The larva when hatched finds the inner wall of the chamber which has been fitted for its temporary abode always provided with the necessary food, and it immediately attacks and devours the juicy tissue with great avidity. The cells which are demolished, wonderful to relate, are replaced almost at once. The cells of the gall-pith remain capable of division as long as the larva in the chamber requires food, and the surface cells which have been devoured in the gall-chamber are soon replaced by new cells from below, just as grass which has been mown down or cropped by cattle in a meadow sends up new stems and leaves. The spheroidal gall arising on the leaves of *Salix incana* (*cf.* fig. 360[9]) has only one chamber, and here the larva lives at the expense of the starch and other food-materials contained in the extremely thin-walled cells which constitute the gall-pith (fig. 360[11]). The larva traverses the chamber in a circle, beginning the destruction of the cells at a certain place and eating on as it continues its peregrination (fig. 360[10]). New cells have already been formed for its nourishment by the time it again reaches the place from which it started.

The hard and cortical layers are modified in very many ways as protective measures against the drying up of the gall in summer on the one hand, and against the attacks of birds and larger animals on the other. For the latter purpose the cortical layer is often fashioned like the pericarps of fruits which have to protect the seeds (*cf.* p. 442). This also explains the bitter substances, hard skin, furry coat, bristling processes, and numerous other protective structures which are developed in and on galls just as on pericarps, and which contribute not a little to the remarkable similarity between galls and fruits. Many peculiar developments on the surface of these fruit-like galls cannot indeed be explained in this way, but, as in so many other cases, we conclude that they must afford some other advantage concerning which our understanding is still at fault.

The external similarity between fruits and solid galls affords us useful points for classifying the latter into groups, which we may name berry-like, plum-like, apple-like, nut-like, capsule-like, &c. The currant gall produced by *Spathegaster baccarum* on the male catkins of the Oak has not only the form and size of a Red Currant berry, but is also succulent and coloured red, and when several of these galls are formed on the same inflorescence it looks at first sight just as if racemes

of red currants had been borne by some chance or other on Oak twigs. The galls produced by the Beech-gall gnat (*Hormomyia fagi*) on the foliage of the Beech resemble small plums, being surrounded by a hard layer which consists of a stone kernel and a layer of cells which might be compared to the fleshy part of a plum. The galls caused by gall-wasps of the genus *Aulax* on the nutlets of many Labiatæ, especially on *Nepeta Pannonica* and *Salvia officinalis* also assume the form of stone-fruits. The insect lays its eggs in one of the four nutlets developed at the base of each flower; and within a week this grows into a smooth greenish-yellow ball which has the external appearance of an unripe cherry. A section through it shows that it possesses also the same structure as a cherry, plum, or stone-fruit in general. The succulent outer layer surrounds a hard stony kernel, but in the cavity of the kernel there lies the white larva of the gall-producer instead of the seed. These galls fall off just like fruits in July, and lie on the ground during the winter; and the mature insect does not bite an opening in the wall of the gall through which it can emerge until the following year. It has been already remarked at the beginning of this section how strong is the resemblance between apple-fruits and the spherical oak-galls, known as oak-apples, which are produced by various Cynipedes (see fig. 364[3]), together with the small red-cheeked galls produced by *Rhodites Eglanteriæ* and *Nematus gallarum* (see figs. 361[2] and 361[7]) on Rose and Willow leaves respectively. Pith-galls which resemble certain dry fruits are very common. Those produced on the green cortex of young Oak twigs by *Aphilothrix Sieboldi* (see fig. 364[1]) remind one of the fruits of species of *Metrosideros*, those produced by *Neuroterus lanuginosus* and *Spathegaster tricolor* on the leaves of the Turkey Oak (*Quercus Cerris*; see figs. 364[11] and 364[14]) have a decided similarity to the indehiscent fruits of the Woodruff and of the Goose-grass (*Asperula odorata* and *Galium Aparine*). The "spangle" galls produced on Oak-leaves by the gall-wasps *Neuroterus fumipennis* and *numismatis* resemble the fruits of *Omphalodes* (see figs. 364[12] and 364[13]), and the galls on the leaves of *Duvaua longifolia* produced by an insect *Cecidoses Eremita* have the form of a capsule which opens by an operculum (see figs. 362[5] and 362[6]). Like fruits these galls may appear in all imaginable conditions with smooth, warted, or rugged surfaces, or covered with woolly or velvety hairs, with bristles or spines, fringes or claws, or even with moss-like outgrowths. The galls with moss-like covering occurring on the Wild Rose have been known from remote times as Bedeguars. They are caused by the Rose-gall wasp (*Rhodites Rosæ*), which deposits its pointed, sometimes hooked eggs early in the spring in the substance of an undeveloped leaf while it is still folded up in the bud. The growth of the leaf becomes altered, the first sign being the development of numerous hairs. The larvæ, when they creep out of the eggs, penetrate deeper into the tissue of the leaf, and it swells out into a solid gall containing as many chambers as there are larvæ. Hairs and fringes continue to form on the exterior till those curious structures are formed which were said to have the power of inducing a peaceful sleep when laid under the pillow. Usually the stalks of the

young bud-leaves are pierced and then the upper portion of the leaf becomes atrophied. More rarely is the egg laid in the epidermis of one of the leaflets, in which case the leaves attain their normal size and only this particular leaflet is decorated with little bedeguars, as shown in fig. 361[1]. When the petioles of three young leaf-rudiments are pierced simultaneously, as often happens, three single galls are produced close together on a shortened axis, and the whole structure may then attain the size of a pine-cone.

The portion of meristematic tissue which is pierced by the insect when it deposits its eggs sometimes remains an open passage; but more often a corky tissue is formed at the wounded spot which quite closes the chamber wherein the larva dwells. Under these circumstances the insect when it emerges must itself make an exit-passage from the gall, and this it does by biting a hole through it with its mandibles (see fig. 364[3]). The gall-wasps (Cynipedes) invariably leave the chamber which has hitherto served them both as a safe habitation and as an inexhaustible storehouse in this way. This does not occur, however, in some of those solid galls which owe their origin to gall-gnats of the genera *Hormomyia*, *Diplosis*, and *Cecidomyia*, for example, in those on the leaf-blade and petiole of the Aspen (*Populus tremula*) produced by *Diplosis tremulæ* and on the leaves of Willows (*Salix Caprea, cinerea, grandifolia*) by *Hormomyia Capreæ*. Here the exit-passage is formed during the development of the pith. The gall consists, as in most other solid galls, of a pith, a hard layer, and an epidermis, but the enormously developed pith and the hard layer do not quite entirely surround the small larval chamber, they leave a small aperture on the part of the gall which is most arched. As long as the epidermis stretches over this place the mouth of the passage is of course not evident, but when the time comes for the insect to quit the chamber a gaping slit is spontaneously formed in the tense epidermis. In many instances the insect or the pupa as it pushes forward may break through the thin skin. A peculiar closure which might be compared to a lid is formed in the common solid galls which are produced so abundantly on Beech leaves by *Hormomyia fagi* and which have been already alluded to. Just as the pupa of many Lepidoptera projects out of the hole in the cocoon which the caterpillar has spun for it far enough to allow the insect to fly away uninjured when it emerges, so that of *Hormomyia fagi* presses through the lid-like closure at the base of the gall, and the winged insect comes out leaving the chrysalis-case behind it.

The opening of some solid galls, which resemble operculate capsules, and which may be termed capsule-galls, is especially remarkable and requires a more detailed description. As long as the larva or grub can remain and obtain food in the larval chamber the gall is completely closed, but when the time approaches for it to move its quarters and to enter the pûpal stage in the ground a circular line of separation is formed in the tissue, and the part of the wall within the circle comes away as a lid. The process is seen very prettily in the gall produced on the leaves of the Turkey Oak (*Quercus Cerris*) by the gall-gnat *Cecidomyia cerris* (see fig. 362[7]). In its closed condition the gall is a firm rounded chamber

so embedded in the leaf that it projects on the upper side as a small pointed cone, and on the lower side as a disc covered with a thick coating of hairs. In the autumn a circular piece like a lid becomes detached from the lower side of the chamber. It corresponds exactly with the extent of the hairy disc, and is so sharply defined that it looks as if it had been cut out with a knife (see figs. 362[8] and 362[9]). The operculum falls off, and the larva which had emerged from the egg and which has lived all the summer in the gall-chamber tumbles out and makes its way into the ground, where it begins to spin. By the next spring it has entered the pupal stage, and the gall-gnat creeps out of the chrysalis about May.

Still more peculiar are the galls produced by *Cecidoses Eremita* on the green

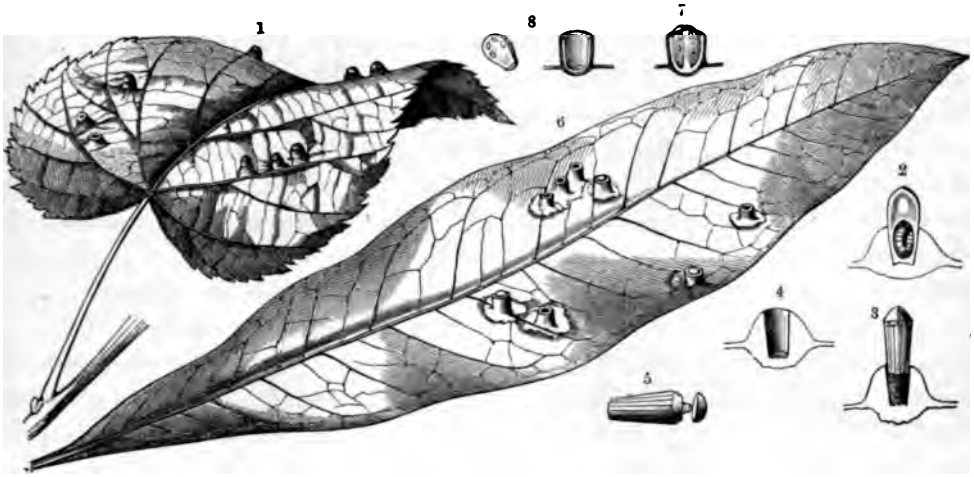

Fig. 363.—Solid Galls.

[1] Capsule-like galls on a leaf of the Broad-leaved Lime (*Tilia grandifolia*) produced by *Hormomyia Réaumuriana*. [2] Longitudinal section through one of the galls, showing the maggot in the interior; × 2. [3] Longitudinal section through a capsule gall from which the inner gall is just being extruded; × 2. [4] Outer gall after the extrusion of the inner gall; × 2. [5] Inner gall at the moment when the operculum is thrown off; × 2. [6] Capsule-galls on the leaf of a Brazilian species of *Celastrus*. [7] Longitudinal section through one of these galls; × 2. [8] The same after the inner gall has fallen out; × 2. [1] and [6] natural size.

cortical tissue of young twigs of *Duvaua longifolia*, a South American representative of the Anacardiaceæ (see figs. 362[5] and 362[6]). The gall is quite spherical and very hard, and its large cavity conceals the caterpillar which has been hatched from the egg. When the time draws near for the formation of the pupa, a plug with a projecting rim is developed on the side of the gall furthest from its point of attachment. When the plug is pushed out a circular hole is left which leads into the gall-chamber through which the caterpillar escapes from its dwelling. People who have not seen these galls with their own eyes might almost think this description was the work of imagination. And yet there are still more wonderful forms in this class of gall-structures. On the foliage of the Lime (*Tilia grandifolia*) a growth arises round the eggs of the gall-gnat *Hormomyia Réaumuriana* which at first has the form of a flat lens inserted in the green tissue of the blade, but which gradually enlarges until it projects from the upper side like a

blunt cone and from the lower as a hemispherical wart. The gall-chamber is inhabited by the maggot of the gall-gnat. The top of the conical part loses its colour in July and becomes yellow and brown, and a rim is formed around its summit. On cutting a vertical section through the gall at this stage it is seen that the tissue forming the wall of the chamber consists of two parts (see figs. 363[2]). The inner layer, which contains the maggot, is surrounded by an outer one which gradually passes into the green substance of the leaf and extends up to the rim just mentioned. The whole structure has separated into an "outer" and an "inner" gall, the inner gall resembling an egg lying in an egg-cup (*cf.* fig. 363[2]). During the summer the inner gall separates completely from the outer and is actually thrown off by it. For the accomplishment of this the tissue of the outer gall swells up very much, so that it exercises a pressure on the inner gall which is shaped not unlike a cone, somewhat narrower below than at the top (see fig. 363[3]). The extruded inner gall falls on the ground below the Lime-tree and assumes a dark-brown colour; the outer gall remains as a little crater embedded in the leaf-blade and ultimately shrivels up (*cf.* figs. 363[1] and 363[4]). The detached inner gall is smooth at the blunt and previously upper extremity, and striated at the other; it is not unlike a detached composite-fruit. The gall-gnat within feeds for a little time longer on the succulent lining, and then rests through the winter; in the spring it makes its escape. To do this it bites a ring-shaped groove below the conical top of the gall and presses against the roof, which, owing to the breaking of the tissues around the ring, comes away like a lid (see fig. 363[5]). A similar state of affairs prevails in a gall formed on the foliage of a Brazilian species of *Celastrus* (see figs. 363[6, 7, 8]), but here the inner gall (which comes away) has several chambers, and the outer gall has the form of a cup set in the green blade.

The place of origin of all these solid galls depends of course upon the insects producing them. These are usually very fastidious about the place where they will lay their eggs, and it is truly astonishing with what care they search out spots difficult of access, and at once favourably situated as regards food supply and likely to afford a safe habitation for their offspring during the larval stages. The small gall-wasp *Blastophaga grossorum* lays its eggs in the ovaries of the "gall-flowers" in the interior of the figs of *Ficus Carica* (see p. 160 and figs. 240[14] and 240[15], p. 157). The gall-wasps *Andricus amenti* and *Neuroterus Schlechtendali* deposit them in the stamens of the Turkey Oak; the gall-wasp *Cynips caput-medusæ* lays hers in the side of the bract-scales which surround the pistillate flowers of the Oak (*Quercus sessiliflora* and *pubescens*), and so produces a gall with innumerable stiff-pointed fringes entangled with one another which ward off the attacks of other animals (see fig. 364[10]). Countless gall-producing insects deposit their eggs on the lower side of foliage leaves, some preferring the lamina, others the veins. *Andricus curvator* prefers the margin of Oak leaves, *Diplosis tremulæ* the petiole of the Aspen at its junction with the blade. Several gall-wasps, as, for example, *Andricus æstivalis* and *Andricus grossulariæ*, seek out the floral receptacle in the male catkins of the Turkey Oak for the deposition of their eggs, whilst

several Cynipedes, e.g. *Aphilotrix Sieboldi* (see fig. 364[1]) lay their eggs in the green cortex of the young twigs. Solid galls are very rare on roots, but they do occur

Fig. 364.—Various Oak-galls.

[1] Solid galls on the cortex produced by *Aphilothrix Sieboldi*. [2] Bud-gall from a foliage-bud produced by *Cynips Hartigii*. [3] Solid galls on an Oak twig produced by *Cynips Kollari*. [4] One of these galls cut in half. [5] Bud-galls from foliage-buds produced by *Cynips lucida*. [6] One of these galls cut in half. [7] Leafy bud-galls produced by *Aphilothrix gemmæ*. [8] Bud-galls from foliage-buds produced by *Cynips polycera*. [9] Longitudinal section through one of these galls. [10] Gall on the pericarp of *Quercus pubescens* produced by *Cynips caput-medusæ*. [11-14] Spangle galls on a leaf of the Turkey Oak (*Quercus Cerris*); [11] produced by *Neuroterus lanuginosus*; [12] by *Neuroterus numismatis*; [13] by *Neuroterus fumipennis*; [14] by *Spathegaster tricolor*.

in this situation in the oak, being produced by the gall-wasps *Aphilothrix radicis* and *Biorhiza aptera*.

When several organs of a plant immediately adjacent to one another are concerned in the production of a gall it is said to be *compound*. Compound galls are for the most part produced from buds, and they are all comprehended under the general name of *Bud-galls*. They are extraordinarily varied in their characters, some being merely abbreviated axes clothed with scale-like leaves, in others only the base of the shoot is involved and above the gall it continues its growth quite normally, whilst in others again the axial portion of the structure is much swollen, and the leaves hardly represented at all. It is difficult to give any satisfactory classification of these bud-galls; still, for the sake of arranging our facts, we may distinguish these types, viz.:—the *ordinary bud-gall*, the *cuckoo-gall*, and *cluster-gall*. Ordinary bud-galls involve several, often all, the members of a shoot. The axis of the shoot is always deformed and abnormally thickened. The swollen portion contains in its interior one or several larval chambers surrounded by a pith-like layer. Two varieties of ordinary bud-gall may be distinguished. The first is leafless; no leaves are present, or, more correctly, they are transformed into tubercles, pegs, and knobs which merge insensibly into the swollen axis which contains the larval chamber. The second possesses leaves, the gall being covered with scale-like bracts or more or less fully developed green foliage-leaves. Amongst the leafless bud-galls the most interesting are those which are armed with special means of protection against the attacks of animals on the watch for the larvæ of the gall-wasps. The gall shown in figs. 364[8] and 364[9], produced by *Cynips polycera* on the leaf-buds of *Quercus pubescens* and *sessiliflora*, which to a certain extent affects a whole lateral shoot, has the form of a young Medlar fruit, and on it may be seen 3–5 metamorphosed leaf-structures projecting as stiff-pointed pegs which gradually pass into the tissue of the shoot axis. This gall is one-chambered, and the tissue of the wall has separated into an outer layer and an inner spherical pithy gall. The gall shown in fig. 364[2] is produced by the gall-wasp *Cynips Hartigii* which lays an egg in the middle of the leaf-bud of the Oak (*Quercus sessiliflora*). The bud does not develop into a leafy shoot, but into a small one-chambered gall with large tooth-like or club-like processes which represent metamorphosed leaves. The thickened angular ends of these projections fit closely to one another so as to form a sort of second outer coat to the gall-chamber through which hostile ichneumon-flies cannot penetrate. The gall much resembles the cone-fruit of a Cypress in the arrangement and form of its superficial processes. The galls produced from the buds of various Oaks (*Quercus pendulina, sessiliflora, pubescens*) by the gall-wasp *Cynips lucida* are still more peculiar (see figs. 364[5] and 364[6]). They contain several larval chambers with abundant pithy tissue, whilst innumerable slender processes resembling limed twigs in being very sticky on the capitate thickened end project from their exterior. Ichneumon-flies and other animals hostile to the gall-producers take good care not to come into contact with these spikes which are to be regarded probably as transformed leaves springing from the swollen axis. Among the galls produced from leaf-buds belonging to this group there are some in which the leaves are merely indicated as tubercles. This is the case, for example, in the many-chambered,

ıgy gall, red-cheeked on the sunny side but pale elsewhere, which is produced he tips of the branches of the Oak by the gall-wasp *Dryoterus terminalis*, and ıs very like a potato in shape. The leaves are only represented by small ill-ned knobs and ridges, just as in the potato. To this class of galls belongs that to which the term "nut" is popularly applied, and even in commerce, the ıe has been transferred from this to the whole of the first group of compound ȝ (bud-galls). The "nut" is produced on the Oak by *Cynips calicis* as an ular and irregularly-grooved gall which originates at the end of a flower axis, the cupule formed of several bract-scales as well as the ovaries are concerned he growth. This class of galls also includes the irregular blunt swellings on en twigs (*Populus tremula*), which are caused by the larva of a beetle (*Saperda ulnea*), and in addition the many-chambered woody "canker cushions" as large nut which are produced on the branches of Willows by *Nematus medullaris*.

The gall shown in fig. 364[7], which arises on various Oaks (*Quercus pedunculata, liflora, pubescens*) by the action of the gall-wasp, *Aphilothrix gemmæ*, may be ːted as a type of leafy bud-galls. It resembles the cone of a Hop or Larch, is developed from a foliage-bud. It has a much-abbreviated swollen axis, whose ıe separates into an inner and outer gall, beset with numerous dry, brown lan-ate hairy scales having the form of bract-scales. Bud-galls which are covered ı green foliage-leaves are produced by the gall-wasp *Andricus inflator* on the , but they are more commonly met with on herbaceous plants, *e.g.* by *Urophora lui* on *Cirsium arvense*, by *Diastrophus Scabiosæ* on several Knapweeds (*Cen-rea alpestris, C. Badensis, C. Scabiosa*), by *Aulax Hieracii* on various Hawkweeds eracium murorum, sylvaticum, tridentatum*, &c.). Usually the foliage-leaves stunted, and not infrequently the blades of some of them are quite obliterated, ıat the gall in that region is only furnished with scaly leaf-sheaths. A Sage wing in the Isle of Crete so often bears leafy bud-galls resembling a small nce-apple, produced by a species of *Aulax*, that Linnæus called it *Salvia pomi-*. The stem of this Sage is swollen out like a ball, and the spherical mass, ːred with a gray felt of hairs on the exterior, is surmounted at the top with a ıp of small wrinkled leaves, which look like the persistent calyx of a Quince-le. The best known and most widely distributed of these forms, found on the wkweeds named above, consist of knob-like swellings of the stem. The larval mber is situated inside the enlarged pith, the ring of vascular bundles, which has ergone much shifting, forms the protective layer, and the cortex of the affected on of the stem forms the cortical layer of the gall. The epidermis is densely ːred with hairs.

Leaving the galls which consist of modified foliage-buds, we pass on to such as ıist of metamorphosed *flower-buds*. They arise from flower-buds in which small -gnats have laid their eggs. The larva hatched from the egg lives in the cavity ıe ovary, or in one of its loculi when there are several, and this space, therefore, ımes the larval chamber. The corolla, which envelops the ovary in the flower-remains closed, like a cap on the top of the larval chamber. The calyx becomes

inflated, enlarged, and sometimes fleshy. The whole gall resembles a bud or small bulb; it is not unlike one of those bulbils which so often arise instead of flowers on the flowering axis of certain species of Allium. They occur especially on the Bird's-foot Trefoil (*Lotus corniculatus*), where they are produced by the gall-gnat *Cecidomyia Loti*, on the various species of Mullein (*Verbascum Austriacum, nigrum, Lychnitis*, &c.) by *Cecidomyia Verbasci*, on several species of Germander (*Teucrium montanum, Scordium*, &c.), caused by *Lactomelopus Teucrii*, and on the Rampion (*Phyteuma orbiculare*), where they are produced by *Cecidomyia phyteumatis*.

Closely allied to these bud-galls are those remarkable gall-structures which are commonly known in Austria as "cuckoo-buds". The cuckoo is supposed to be concerned in their formation, just as it is in that of the frothy saliva-like masses deposited by the *Cicada* on the Cuckoo-flower (*Cardamine pratensis*). The name "cuckoo-galls" may be employed for the whole of this sub-group. They are characterized by their pale whitish colour, soft spongy tissue, and especially by the fact that they only involve the *base* of the shoot, while the upper end can continue its growth unaltered. In this respect they may be compared to a Pine-apple fruit, where the axis rises above the fleshy collective fruit (*cf.* p. 436) as a green leafy tuft, which does not lose its growing power even with the ripening of the fruit. The history of the development of cuckoo-galls is probably like that of covering galls; and the main distinction lies in the fact that in the former the gall is produced not merely from a *single* organ or some part of it, but from a *whole group* of adjoining plant-members. The best known and most widely distributed gall of this group is produced by the pine-apple aphis *Chermes abietis* on the twigs of the Spruce Fir (*Abies excelsa*, see fig. 362[1], p. 534). Early in the spring, before the foliage-leaves have begun to unfold, the parthenogenetic females, the foundresses of the colony, attach themselves each to the base of a young leaf and lay a mass of eggs at the spot to which they have adhered. The larvæ, hatching, penetrate the surrounding parts of the shoot with their beaks; the shoot swells, as do the bases of the needles, and a growth, the Spruce gall or Pine-apple gall results. The gall somewhat resembles a small Fir-cone about an inch long, with the surface divided into small convex areas, each bearing a short needle-like projection in the middle; these are the deformed needles, which, becoming swollen, touch each other on the outside of the gall. They are separate inside, so that the gall contains a series of cavities or chambers. In these chambers the larvæ live in numbers, either entering the chambers during the growth of the gall or being inclosed by the swelling of the surrounding needles—this point is not certainly determined. They remain in the small cavities so formed and feed, cast their skins, and multiply there. In August the gall begins to dry up, each of the small cavities opens by a slit in front of the green needle-point surmounting the cushion (see fig. 362[1], p. 534), and the winged insects now leave the place in which they have passed the spring and summer.

Cuckoo-galls are met with almost as frequently on Stellatæ, viz. on various species of Bedstraw (*Galium Austriacum, boreale, uliginosum*, &c.) and Woodruff

(*Asperula galioides, tinctoria*, &c.) as on Fir-trees. The infected parts of the shoot remain stunted, and white spongy cushion-shaped growths, which are somewhat grooved, arise at the bases of the leaves. Since the growing tissues of neighbouring leaves touch one another the grooves or channels form small cavities in which live the larvæ of the gall-producing gnats (*Cecidomyia Galii* and *Asperulæ*). In the common Bedstraw (*Galium Mollugo*) these spongy growths arise, not from the bases of the leaves, but from the green cortex of the stem round the insertion of the leaves and lateral branches. They rise up as cushions and lobes, and several join together to form a sort of dome, under which the larvæ of the gall-gnat dwell. The foliage-leaves are scarcely altered in form, and when lateral twigs arise from the place they also are unchanged. It not infrequently happens that short lateral axes terminated by flowers spring up quite unmodified above the spongy white cuckoo-gall. Cuckoo-galls also occur on Cruciferæ, viz. on *Barbarœa vulgaris*, *Nasturtium palustre, sylvestre*, and *Sisymbrium Sophia*. They are produced by *Cecidomyia Sisymbrii*, and originate principally at the bases of the flower-stalks half-way up the inflorescences. They look like spongy white bodies which surround the pedicels like the brim of a hat. As the growths from neighbouring pedicels meet together they roof over chambers which serve as habitations for the larvæ of the gall-gnats. Viewed from outside the galls appear like irregular white bodies inserted in the inflorescence, which remind one of the fruit of the white Mulberry-tree.

The term *cluster-gall* is reserved for that type of bud-gall in which the axis is much restricted or stunted and covered with densely crowded leaf-structures; it is in the chinks and recesses between the crowded leaves of these galls that the insects concerned pass the whole or a portion of their lives. The animals which cause the galls belong to very different classes. Gnats, leaf-fleas, leaf-lice, and mites are the commonest varieties. The gnats only live in the galls during the egg and larval stages, but the others pass their whole life there. They invariably settle on the end of a shoot while it is still undeveloped in the bud. The axis of the shoot remains more or less stunted in consequence of the influence the animals exercise on it and its leaves undergo fundamental alterations. The blade or sheath of the leaf is deepened and hollowed to afford sufficient space to the animals which have established themselves between them, and as these parts of the leaves touch one another recesses are formed not unlike those which are developed in fir-cones for the growing seeds. The sheathing part of the leaf is often rather thickened, and its succulent cells serve as food for the animals living in the gall; in other instances the hollowed leaf-blades are thickly covered with hairs, and this coat then has the same significance with regard to the insects as the felt of hairs on isolated leaves already described. Very different forms of galls are produced according as to whether the free ends of the leaves turn back or remain in contact, and whether the axis from which the leaves spring is more or less contracted. Sometimes they remind one of open rosettes, sometimes of closed balls, bunches and tufts, sometimes of pig-tails and witches' brooms.

Clustered galls may be divided into two classes, those which develop in the region of the *flowers* and those in the *foliage* region respectively. The most noticeable and best known forms of the galls occurring in the foliage region on rudimentary leafy shoots are the following:—First, those peculiar structures on the tops of Willow twigs (*Salix aurita, Caprea, grandifolia,* &c.) which are popularly termed "Rose Willows". They are caused by the gall-gnat *Cecidomyia rosaria.* The leaf-bud from which they arise keeps its axis quite short and develops on it numerous green leaves arranged like the petals of a double rose. The lowest leaves of the "rose" differ but slightly from the normal foliage of the particular species of Willow. Usually there seems to be only a shortening and broadening of the petiole and leaf-sheath, the green blade being almost unaltered. In the upper inner leaves, however, the sheath-like part of the leaf is much increased in size, and nearer the centre of the "rose" the leaves become scale-like. The leaf-blade has entirely disappeared, and the end of the contracted axis possesses only the remains of leaf-sheaths. It is worth noting that the number of leaves in a Rose Willow is always greater than would be found on an unaltered shoot of the same species. For example, if the number of leaves on the one-year-old shoot of the Sallow (*Salix Caprea*) is 25, the number in a "rose" on the same species would be at least twice as large. This can only be explained by supposing that a "prolepsis" has occurred, *i.e.* that not only the shoot laid down for the current year has developed, but also one originating from a bud of this shoot, which, under normal conditions, would not have developed until the following year. When autumn comes the rosette-shaped galls on the Willow bushes show up conspicuously at a distance because the leaves forming them do not fall off like the rest, but remain behind as brown dried structures at the ends of the branches. They are also found associated with the catkins. The rosette-shaped galls produced by the gall-gnat *Cecidomyia cratægi* at the tips of Hawthorn twigs (*Cratægus Oxyacantha* and *monogyna*) also claim attention. They are full of bristles and resemble tiny birds' nests. The stimulus of the gnat larvæ excites a deeper and more frequent segmentation in the leaves and stipules. Narrower points and fringes which are much bent and which resemble the antlers of reindeers replace the broad lobes. Also soft spines with capitate ends rise up from the green cortex of the twigs and from the tissue of the leaf-blade, especially above the vascular bundles, and 3–5 of them often fuse together into cock's-comb-like structures. These bristling rosettes on Hawthorn branches also remain long after the time the ordinary foliage falls off.

In marked contrast to the rosette-like cluster-galls are others whose leaves all fold together in a ball something like the leaves of a cabbage, the whole gall having a button-like appearance. The outer leaves are round and hollowed on their upper side, and they usually fold together like mussel-shells. The inner leaves have a similar form, but they are much smaller and more concave, and they have become succulent and paler in colour. The galls produced by *Cecidomyia genisticola* on *Genista tinctoria* and those which *Cecidomyia Veronicæ*

gives rise to on *Veronica chamædrys*, and which gall-mites produce on the Wild Thyme (*Thymus Serpyllum*; see figs. 360[4] and 360[5], p. 531), form white buttons on the ends of the shoots which show up conspicuously from the dark green of the surrounding foliage. The white colour is due to the fact that the outer leaves, which fold together like mussel-shells, are thickly covered on the outside with white hairs. *Cecidomyia Artemisiæ* produces on the branches of *Artemisia campestris* a closed cluster-gall which is cased in white wool like a shroud. On the other hand, the large, button-shaped, closed cluster-galls which are produced by *Cecidomyia rosaria* on Willows (*Salix purpurea*, &c.) and by a gall-mite on the spikes of the Brome-grass (*Bromus*) are green and smooth, or at least they have not more than the usual number of hairs.

On the shoots of the Yew (*Taxus baccata*), the Flax (*Linum usitatissimum*), *Euphorbia Cyparissias*, the Moss Campion (*Silene acaulis*), and several Ericas (*Erica arborea, carnea*, &c.) the influence of various gnats (*Cecidomyia Taxi, Euphorbiæ, Ericæ, scopariæ*, &c.) produces galls with linear erect leaves crowded together into tufts. The base of the crowded leaves and the axis of the gall are usually rather thickened, so that it looks as if the linear leaves were set on a rounded button, and this is particularly marked in *Euphorbia Cyparissias*. This division includes the gall formations occurring on Juniper twigs (*Juniperus communis*), which are caused by the gall-gnat *Lasioptera juniperina*. The acicular leaves of the Juniper are arranged in whorls of three on normal shoots. By reason of the influence of the gall-gnat *Hormomyia juniperina* the whorls at the top of the twig become so changed that the last but one represents a cup bordered with three teeth in consequence of the broadening of the needles, while the terminal whorl is metamorphosed into a dwelling surrounded by three short leaflets. This gall closely resembles the cone of the Arbor Vitæ (*Thuja occidentalis, orientalis*, and *plicata*) in form.

An insect, *Livia Juncorum*, produces galls on various Rushes (*Juncus*), especially *Juncus alpinus* and *lamprocarpus*, which look like knots or tassels. The axis of the shoot is contracted, the sheathing portions of the leaves which cover one another are much widened, and the colour is pale except where it is reddened by exposure to the sun; their appearance is like the outer covering or top of a tassel. The stunted green blades which spring from the sheathing portions are thread-like and arranged as the loose strands of the tassel. Not infrequently short lateral shoots arise in the axils of some of the leaves, and then the whole structure looks like a bunch of tassels.

Closely allied to these cluster-galls on the stems of Rushes are such as resemble tufts and witches' brooms, produced by mites on the branches of hairy Willows, especially on the white Willow (*Salix alba*). Instead of the long leafy Willow rod which would have emerged under ordinary circumstances from a foliage-bud, a confused mass of twigs with short leaf-scales is developed which at first seems a perfect mystery. By careful examination it is seen that the axis of the shoot laid down in the bud has remained stunted, and that lateral

shoots have developed from the axils of its leaves. These lateral shoots again develop lateral axes in the axils of their leaves, and so on to the third, fourth, and fifth degree. Thus, in the course of a month, shoots have unfolded, which, except for the influence of the gall-mites, would not have followed one another for three, four, five, or even six years, and therefore these galls afford us another instance of what has been termed "prolepsis" or precocious development of structures which would not yet arise. Of course all the axes of these shoots are dwarfed and the leaves which clothe them are diminished in size. The shortening and diminishing increase gradually, so that the axes and leaves of the fourth and fifth degree are much smaller than those of the second and third. The last lateral shoots remain bud-like, and their small scaly leaves fold over one another like the bracts in the involucre of a Composite. The "witches' brooms" which are caused by gall-mites on Lilac (*Syringa vulgaris*) and Privet (*Ligustrum vulgare*) bushes are similar in nature to these closed galls on the Willows. Frequently the metamorphosis of the leaves on the axes of the third, fourth, and fifth degree includes those of the floral region, and such cases form to some extent a bond of union between cluster-galls on foliage and on floral regions, respectively.

One of the most remarkable changes exhibited by the gall-structures just mentioned, viz. the abbreviation of the axis, is of course not to be noted in cluster-galls in the floral region. The part of the axis which forms the floral receptacle does not grow into an elongated shoot, but always remains short, and the floral-leaves it bears stand close to one another, forming whorls in whose niches and recesses numerous small animals can hide. But these animals effect other very marked alterations by their stimulus. In some flowers, instead of the normal red, blue, white, or yellow petals, green leaflets appear which resemble foliage-leaves in character, and then we say that the flowers have become "green" or "leafy". In other plants the stamens are transformed into petals, and the flowers are said to be "double". Finally, it may happen that the carpels which are usually united together to form a syncarpous ovary stand on the receptacle as distinct structures, and that to a certain extent their union has been dissolved. In these cases we speak of "antholysis" (*cf.* p. 80). The influence of gall-mites also produces metamorphosed flowers which may be both green and double, and in which the pistil may have separated into its individual carpels.

The best flowers for observing these metamorphoses in all imaginable degrees are the small-flowered species of the Chickweed genus (*Cerastium macrocarpum, triviale*, &c.), several Caryophyllaceæ (*Lychnis Viscaria, Saponaria officinalis*, &c.), Cruciferæ (*Cardamine uliginosa, Camelina sativa, Lepidium Draba*), Gentians (*Gentiana acaulis, rhætica*), Speedwells (*Veronica officinalis, saxatilis*) and Milfoils (*Achillea Millefolium, nana*). In Speedwells the petals come to resemble leaves. The bunches, rosettes, and balls of small green leaves replacing the flowers are set close together on the rachis of the inflorescence and form green racemes and tufts, sometimes even small witches' brooms. In *Veronica saxatilis* the rachis of the raceme, the pedicels, and the bracts are covered with hairs, which

is not the case when the plants are free from the mites; the foliage-leaves in the neighbourhood of the raceme are also lobed and deeply indented, which again is not the case in uninfected plants of this species. In the capitula of the above-named Milfoils the peripheral ray-florets as well as the central tubular ones become leaf-like, and this gives rise to the most peculiar forms. A capitulum is often separated into several stalked sub-capitula, the flowers being metamorphosed into green funnels with jagged mouths, and into small flat-lobed and toothed foliage-leaves, whilst short, green, scale-like leaflets rise from the midribs of these leaves representing the metamorphosed stamens. A very remarkable "doubling" produced by gall-gnats is to be observed in flowers of the Alpine Rose (*Rhododendron ferrugineum*). The stamens and carpels are changed into red petals by their influence. Since *Rhododendron* flowers have ten stamens and five carpels, there should be only fifteen red leaflets in the centre of each, but as a matter of fact there are double and treble as many, and there has been not merely a metamorphosis but also a multiplication of the leaves. The flowers of some plants which belong to the Valerians, especially of the Corn-salad (*Valerianella carinata*), of which a small umbellate cyme is shown in fig. 358 [2], p. 523, are doubled by the influence of a gall-mite, but without any multiplication of the petals. The doubling is restricted to the transformation of the stamens into a whorl of petals. But we also have another peculiar alteration. The petals become enlarged to more than fifty times their normal size, and change into fleshy lobes which are fused with one another into a disc. As all these lobes bend back, and become concave below, cavities are formed under the flowers in which the gall-mites can dwell (see fig. 358 [3], p. 523).

The axis of the inflorescence and the stalks of single flowers are often thickened and fleshy in these cluster-galls, and they are also stunted and bent in the most varied manner. If several neighbouring pedicels fuse together, structures like cocks'-combs, or like a compressed and flattened branch, arise; to these the term *fasciation* is applied. Sometimes when numerous pedicels arranged in the form of umbels fuse together we have structures like coral-colonies, or irregular clumps which are beset with green flowers usually much reduced in size. This is the case in the fasciations of the Ash (*Fraxinus excelsior* and *Ornus*), which are caused by a gall-mite (*Phytoptus*), and which occur so abundantly that it looks as if the tops of the trees had been sown with them.

The enumeration, here, of various forms of galls commenced with the inconspicuous felt-galls on the under side of isolated foliage-leaves, and it ends with the complex cluster-gall, in which hundreds of flower-stalks and leaves are frequently concerned. Of course, only types of the individual groups which have been mentioned in this long series could be instanced, and we cannot make any attempt to describe all the gall-structures at present known, about 1600 in number. Whether the extension of gall-researches in tropical regions will yield new forms which stand outside the pale of the classification given it is difficult to say. Apparently this will not be the case. Perhaps thousands of hitherto unknown galls might be added

to the list, but we should expect that they would fall under one or other of the above-mentioned groups.

Gall-structures have a peculiar significance for the section of the *Natural History of Plants* which deals with the question of the origin of species, since they show most distinctly how fundamental deviations from the original plan of construction may occur in the adult condition of a portion of a plant.

We must be careful to remember always that the immense variety of structures which we call galls would not have existed except for the effect produced on the plants by mites, leaf-lice, gnats, wasps, &c. The foliage of *Rhododendron* would not have been rolled up, but quite flat, if gall-mites had not been present; the branches of *Pistacia Lentiscus* would have borne pinnate foliage with shining dark-green leaflets and not fleshy-red pods if they had not been attacked by leaf-lice; the leaf-bud of *Quercus pubescens* would have developed into a long leafy shoot instead of a body like a medlar if the gall-wasp *Cynips polycera* had not provoked the change; the foliage of *Veronica saxatilis* would not have been lobed like a hand, but would have had a slightly sinuous margin; and the upper leaves of *Thymus* would have been green, spoon-shaped, and smooth on the surface instead of circular and covered with white hairs, had no gall-mites settled on them. The flowers of *Rhododendron ferrugineum*, *Lychnis Viscaria*, *Veronica*, *Cardamine*, &c., would not have "doubled", and the stamens would not have changed into petals, if they had not been under the influence of gall-mites.

Of course, the influence of the animals can only produce these effects on parts of plants which are in an embryonic condition. Mature stems and leaves may be eaten and destroyed by insects, but they can no longer be metamorphosed. But the undifferentiated rudiments upon which the influence is effective are, so to speak, formless. Leaves, stems, and fruits arise from tissue-masses having the form of tubercles and cushions, and each tubercle or cushion originates from a few cells which give no indication of what is to develop from them. Nevertheless, experience teaches us that the plan of construction for the plant-member proceeding from these primitive forms is definitely laid down from the beginning for each species, and the idea that the plan of construction is rooted in the specific constitution of the protoplasm of the plant—*i.e.* in the cell or cells which form the primitive stage or rudiment of the developing leaf, stem, &c., is confirmed. If an alteration in this plan of construction is produced by these animals, it can only be by some alteration of the specific constitution of the protoplasm.

How the alteration is effected is just the puzzle which is at present occupying the attention of naturalists. Once it was thought that the formation of galls was the result of injuries caused in the growing tissue by the ovipositor or sucking organ of insects, but recent investigations have not confirmed this view. The cells actually injured by the insect in laying its eggs perish, and consequently lose power of metamorphosis or of producing modified daughter-cells. Cork, closing over the wound, is always formed from the adjoining living tissue, but for a h

time no gall is produced. The eggs deposited in the tissue, or attached to it, are also incapable of directly inciting gall-formation. There is no marked alteration in the neighbourhood until the grub or larva leaves the egg and excretes a fluid substance. Then growing cells of the most varied description are formed adjacent to the larva, and these rapidly assume the peculiar forms which have just been described. This, of course, applies also to cases where the larva has been hatched from the egg at some distance from the spot and has had to seek out a tissue suitable for its dwelling, as also to instances where adult gall-mites and leaf-lice choose out a suitable place for the deposition of their eggs and then secrete a fluid round them when they lay them. If the animal dies, the growth and renewal of the tissue immediately ceases. The cells round the dead body turn brown and die, so that we may conclude the formation of the gall to be due solely to the substance excreted by living animals.

Those who investigate galls consider that it is chiefly the acrid "saliva" excreted by the larvæ to liquefy their food which acts on the cell-tissue of the dwelling they have selected, but there is no doubt that other excretions may also take part. The chemical composition of this substance is unknown, but we shall hardly be wrong if we include it in the group of nitrogenous compounds called enzymes which were discussed at vol. i. p. 464. Enzymes have the power of altering and decomposing substances, even through the cell-wall, and in this way we can account very simply for a whole series of otherwise inexplicable phenomena in the formation of galls. Moreover, urea or closely-allied nitrogenous compounds may be excreted, so that there is nothing to be said against the view that some of the substances diffuse into the interior of the plant-cells. It is at least certain that the fluid substances excreted by the gall-producing animals, in whatever way they influence the protoplasm in the plant-cells, do not kill it, but actually stimulate it to an extraordinary new activity directly demonstrated by the production of tissues with a definite external form.

Observation shows that these tissues are formed and fashioned differently from what they would have been without the influence of this substance. It follows, therefore, that the substances excreted by the animals have the capacity of affecting in some way the specific constitution of the protoplasm which determines the species in the plant-cells influenced by them. It is specially interesting to note in this connection that it not only is the protoplasm of the cells directly acted on by the excretion which is stimulated to an altered form of constructive activity, but that this stimulus is transmitted from cell to cell in ever-widening circles. The spruce-fir aphis *Chermes abietis* attaches itself firmly by its beak to the scale of a Fir bud, and can directly influence only a few cells of the young shoot hidden in the bud. Nevertheless thousands of cells on this shoot soon begin to assume an altered form, a proceeding which reminds us strongly of the action of a ferment (*cf.* vol. i. p. 505), and also brings to our mind the influence exerted by the spermatoplasm on the ovary. The spermatoplasm is only directly concerned with a few cells in the ovule, but these propagate the influence on all sides to

the carpels and to the receptacle, and sometimes even to the flower-stalk. All these parts would not have developed as they have done had it not been that the minute quantity of spermatoplasm of a pollen-grain had united with a minute cell in the ovule.

It will be convenient to consider here the already mentioned similarity between galls and fruits. If the leaf-rudiments in the bud of a *Pistacia* shrub are not affected by leaf-lice they develop into shining green pinnate foliage-leaves; but if the protoplasm in some of the cells has been altered by the excretions of *Pemphigus cornicularius* this same rudiment will assume the form of a carpel, and become fashioned into a hollow body deceptively like a pod. The fact that the *Pistacia* shrub bears plum-fruits and not pods makes it still more remarkable, for the structure arising from the effect of the animal's excretion, when mature, is not like the fruit of the *Pistacia*, as we should naturally have expected, but like that of a completely different plant species, viz. the Carob (*Ceratonia Siliqua*). The same is true of the metamorphosis caused by the excretion of a gall-gnat (*Lasioptera juniperina*) on the uppermost leaves of the Juniper (*Juniperus communis*) which assume a form very like the fruit of the Arbor Vitæ (*Thuja*), and many other instances might be mentioned in which galls are produced in certain species of plants by animal excretions, looking outwardly very like the pods, capsules, nuts, drupes, and berries of other species. This resemblance to certain fruits is rendered the more pronounced by the development upon the galls of pigments, wax-like excretions, and hairy coverings, but of course they contain no seeds in their interior—only the larvæ of the animals whose excretions produce the changes of form. The wonderful thing is that the metamorphosis of the growing tissue into a fruit-like body is always of the greatest advantage to the animal which has settled in it, since the tissue serves not only for dwelling and food but also for protection against unfavourable weather and against the attack of foes.

It is also a fact of great importance that different animals produce differently shaped galls on the same plant. The Bedeguars produced by *Rhodites Rosæ*, the pea-like galls produced by *Rhodites eglanteriæ*, and the clustered protuberances produced by *Rhodites spinosissimæ* may all occur side by side on the same rose-leaf (see figs. 361 [1, 2, 3] p. 533). On the same elm-leaf *Schizoneura Ulmi* produces a wrinkled gall, *Tetraneura Ulmi* a pocket-gall, and *Tetraneura alba* a covering gall (see figs. 361 [4, 5, 6] p. 533). The spherical gall of *Nematus gallarum* and the bladder-like gall of *Nematus vesicator* occur close together on the foliage of the Purple Willow (see figs. 361 [7] and 361 [8]), and one sees Oak-leaves on which the small spangle-galls of four different gall-wasps, viz. *Neuroterus lanuginosus, numismatis, fumipennis*, and *Spathegaster tricolor* are all present together (see figs. 364 [11, 12, 13, 14] p. 541). It has been shown that some Oaks, for example, *Quercus pedunculata*, may bear as many as 20–30 different forms of gall produced by as many kinds of gall-wasps. The characteristic shape, colour, and hair-covering of these forms of gall is so constant that we can state with certainty what gall-wasps have given rise to them. These facts force us to the conclusion that the fluids

excreted by different gall-producing insects are specifically distinct. It is only in this way that we can account for the fact that the same vegetable protoplasm is incited in one case to produce a fleshy covering gall, in another a hollow pocket, and in a third a closed gall-apple as dwellings for the particular insects concerned.

It should also be mentioned that the same species of insect produces very similar but slightly different galls on different plants. For example, the gall produced by *Nematus pedunculi* on the lower side of the white-haired leaves of *Salix incana* is covered with a white felt of hairs, that which the same gall-gnat produces on the smooth leaves of *Salix purpurea* is smooth; the gall produced by *Rhodites Rosæ* on the light green leaves of *Rosa canina* is pale yellow and somewhat reddened on that side turned towards the sun; that on the violet leaves of *Rosa rubrifolia* produced by the same insect-species is dark violet, &c. These distinctions, though only insignificant, show how certain external characteristics founded in the specific constitution of the protoplasm of different plant-species find expression even in the gall-structures.

These facts confirm the view that the fluids excreted by different species of insects, as well as the protoplasm of each plant species, have a peculiar composition. It is then quite obvious that the alteration which the protoplasm of a species of plant undergoes under the influence of a specific fluid will be subject to definite laws. The protoplasm of the particular plant-cell receives by reason of the alteration, as it were, a new definite constitution with tendencies not the same as before; but since this constitution determines the outer form of the tissue derived from these cells, the tissue itself will become shaped into a particular specific form. These conclusions are of importance with respect to the question of the origin of new species, inasmuch as they throw some light on the processes which lead to the origin of new forms. We can now say that the alteration in the form of a plant only occurs if the constitution of the protoplasm which forms the starting-point of the plant is itself first altered.

The structures known as galls have not the power of maintaining and multiplying themselves, but when their task is ended they perish. In other words, the progeny arising from the seeds of a plant beset with galls exhibits none of the alterations shown by the members or shoots of the parent plant. If, for example, an Oak which is covered with galls is propagated by seeds, the offspring show no trace of the structural alterations exhibited by the branches, foliage, or flowers of the mother-plant. The only change which is perhaps sometimes retained in the offspring is the metamorphosis of the stamens into petals, which has long been known as doubling, and perhaps also the formation of fasciations, &c. in the floral region, as in Cabbages (where it is known as a Cauliflower). Few attempts have yet been made to investigate this matter. My own knowledge of the subject is restricted to some observations made on the Speedwell *Veronica officinalis*. Plants of *Veronica officinalis* which in consequence of the settlement of gall-mites on them produced double flowers in 1877 in the garden of my country house were planted close beside others free from gall-mites and with normal flowers. In the

following year the gall-mites settled on the latter also, and the greater part of their flowers then became double. The same result was obtained after living gall-mites were transferred by me to isolated plants of *Veronica officinalis* with single flowers. These in the following year also bore some double flowers. Fruits with ripe seeds were only produced from the flowers which had remained single amongst the double ones; and the plants which grew up from these seeds always bore single flowers only. The gall-mites disappeared for some unascertained reason—probably they died in the winter. *Veronica officinalis* has only two stamens in each flower, and in the double flowers both these and the two carpels are changed into petals so that of course we could not expect fruit and seeds from them. It would not be impossible, however, that flowers of other plant families which are provided with a large number of stamens might behave differently. It might happen, for example, that only *some* of the stamens would be changed into petals by the gall-mites, and that the carpels would remain capable of fertilization. If on such plants fruits and seeds capable of germination should ripen, the latter might perhaps produce plants with completely and half double flowers. This would be explained by supposing that the alteration undergone by the protoplasm of the cells in the outer part of the flower had extended to the inner, especially to the ovules and seeds, and further to the plants proceeding from these seeds. I would therefore not undertake to state that the Stocks (*Matthiola annua* and *incana*), the Wallflower (*Cheiranthus Cheiri*), the Pinks (*Dianthus Caryophyllus, plumarius*, &c.), the Poppies (*Papaver Rhœas* and *somniferum*), various Ranunculaceæ (*Delphinium, Pæonia, Ranunculus*), and many other plants which have long been cultivated in gardens with semi-double flowers, and which produce such flowers when propagated by seeds, had not gained this characteristic in the first place by the influence of gall-mites. It is less probable, though not beyond the range of possibility, that by the grafting of Hawthorn branches whose uppermost leaves have been deeply segmented by the influence of the gall-gnat *Cecidomyia Cratægi*, a Hawthorn bush might be produced which would exhibit these deep segmentations and slits on all its foliage. However, these last remarks are the merest suppositions; at present we have not the data on which to base any definite conclusions.

THE GENESIS OF NEW FORMS AS A RESULT OF CROSSING.

The aim of agriculturalists has always been so to cultivate their land as to rear plants likely to grow luxuriantly, to bear good fruit, and thus to afford an abundant harvest in return for their pains. Gardeners similarly have made it their endeavour to produce from wild plants races whose flowers are superior to those of the ancestral stock in form, colour, and scent; and the results of their labours are the delight and admiration of all lovers of beauty. In both cases the idea has been to perfect and "ennoble", and the means adopted have been successful to a degree calculated to amaze anyone who studies the history of cultivated plants with attention. The methods which led to these results have not always been deliber-

ately adopted, nor have they depended on scientific researches. On the contrary, chance observations made by growers in the course of their dealings with vegetable life as it occurs in nature have been the means of suggesting the first unaided attempts to make crops more productive, fruits and vegetables more palatable, and flowering-plants more pleasing to the eye.

The most important method adopted has been the artificial crossing of the species which are brought under cultivation. When we consider that, from time immemorial, Chinese and Japanese gardeners have produced Asters, Chrysanthemums, Camellias, Pinks, Peonies, and Roses, of which the majority are the results of crossing, we may assume with certainty that the practice of dusting flowers of one species with the pollen of another species first came into use in those countries. It is true that in Europe the contrivance was known to rose-growers at the time of the Roman Empire, but it was not employed on an extensive scale till the seventeenth century, when the fashion for breeding Tulips and Auriculas became the rage. The gardeners of that day still made a great secret of their mode of procedure, and it was not till the latter half of the eighteenth century that the production of new forms of plants by the aid of artificial crossing was carried on at all generally. For some decades the rearing of these new forms, which are called *hybrids*, has been one of the most important parts of a gardener's duties, and we shall not exaggerate if we put the number of hybrids hitherto produced in gardens in the course of the nineteenth century at 10,000. Many hybrids which were great favourites only a short time ago have disappeared from our gardens and have been replaced by others. As in so many other matters, the fashion changes; new forms are in constant request, and horticulturists endeavour to meet the demand by introducing wild plants from the most various regions and crossing them with those already under cultivation. It is now no longer uncommon for gardeners, in advertising some plant which has been brought from distant parts, to recommend it to the trade, not on the ground of its own beauty, but because it possesses flowers of an exceptional colour or leaves of a peculiar cut, and will therefore, in all probability, if crossed with other species, yield handsome new hybrids. Rose-growers always welcome the discovery of any instance of variation in the Wild Rose as an important event, because, by crossing this Rose with others, they are able to produce a large number of new forms, and there is always the chance that one or other of them may find favour with the public. On an average, 60 newly-bred Roses come into the market yearly; in the year 1889 the number even amounted to 115! A Rose cultivator at Meidling, near Vienna, grows in his garden nearly 4200 different kinds of Rose, and yet he is still far from possessing all the forms which have been produced in recent times (chiefly by French growers) by crossing one with another. According to his estimate, the number of Tea and Indian Roses alone is nearly 1400, and the total number of all the different Roses which the trade has produced up to the present day amounts to 6400.

The plant-forms which are called into existence by the operation of crossing are, in the case of Roses, reproduced largely by means of brood-bodies (cuttings and

layers) as well as by budding and grafting (see vol. i. p. 213); but the *first origin* of the new forms is always to be traced to crossing. This statement applies also to many other plants of which gardeners have taken possession, and especially to cases where propagation by seed requires more time and trouble than multiplication of brood-bodies. The kinds of Tulip, Gladiolus, and Lily produced by crossing are propagated most easily by means of bulbs, and the tuberous Begonias, Dahlias, and Gesneraceæ by tubers, whilst Pinks, Pelargoniums, Cactuses, and many others are most rapidly reproduced by cuttings. Moreover, these methods ensure the preservation of the peculiarities of the new forms unchanged, and such perpetuation of characteristics would be much more difficult to achieve if the plants were propagated by means of seeds. On the other hand, a number of new forms which have originated as the results of crosses effected in gardens, such as those of *Petunia*, *Portulaca*, and *Viola*, are reproduced with less trouble and greater rapidity by seeds, and that method is in such cases preferred to the cultivation of brood-bodies.

The statement that new forms of plants are bred originally in gardens by any other method than that of crossing is incorrect; it is sometimes made in ignorance, but sometimes also with the intention of deceiving. In former times gardeners believed that, in order to produce new forms, it was sufficient to plant different species in close proximity to one another. The idea was that if the seeds of such plants were taken and sown in good soil, there would always be found amongst the seedlings a few forms differing from the parent; these were to be selected for especial care in cultivation, and were to be treated as starting-points of new forms. The gardeners who acted on this assumption had not, it is true, themselves crossed the flowers; and if this was all they meant, there was no falsehood in the statement. The operation of crossing was, however, performed without their knowledge by hive- and humble-bees and other insects, and the planting together of the different species was only of advantage inasmuch as it facilitated the conveyance of pollen from one species to the stigmas of another. A celebrated grower of the old school once assured me, in all seriousness, that he did not himself cross the plants he reared, but that he had repeatedly observed that early in the morning, soon after a flower opened, it put forth infinitesimally fine threads which radiated in all directions and reached across to the flowers of other plants, forming in a short time a web like that of a spider! I would not have mentioned this statement were it not for the importance of pointing out the unreliable character of so many of the statements made by gardeners, especially in the past; and I repeat that the person responsible for the above communication is a well-known and much-esteemed horticulturalist. Gross inventions such as the above would, of course, be at once seen through and rejected by any thoughtful man; nevertheless, in some instances, reports of growers, likewise untrue or inaccurate, but not bearing the stamp of improbability so plainly upon the face of them, have been credited and have even found their way into books, particularly into those whose authors have omitted to confirm the reports by watching the garden-experiments from beginning to end themselves. The statements are then not infrequently quoted as "results obtained

by trustworthy experiments made by gardeners" and relied upon for the foundation of "laws based upon facts"; theories are then built up upon them, and are copied from one book to another. It becomes very difficult afterwards to get rid of such propositions, especially if they afford support to the hypotheses of distinguished *savants*.

An instructive example of the kind of thing referred to is afforded by the following statement which for a long time obtained currency in works on Botany: "Hybrids resulting from the crossing of two species exhibit two forms, in each case, according as the pollen employed in generating them belongs to the one or to the other species." There are, of course, two ways in which a pair of species, which may be represented by the letters A and B, may be crossed. In one case the pollen from A is transferred to the stigma in B, whilst in the other case the pollen is taken from B and transferred to the stigma in A. Now, it has been asserted that it is possible to determine from the form of the hybrid which of the two parent-species supplied the pollen. The hybrid is said to resemble that parent more closely from which the pollen was derived so far as its flowers are concerned, but to show greater affinity to the fertilized stock in respect of its foliage. This is, however, absolutely untrue. All careful experiments made without prejudice have pointed to the conclusion that it makes no difference to the forms, either of the leaves or of the flowers, whether the pollen has been taken from the one parent-species or from the other. Besides this, in most instances the approximation of the hybrid-form to one or the other stock affects all parts of the hybrid plant in an equal degree, and not the flowers or the foliage only. In the rare cases where a hybrid has flowers more like those of one parent and leaves more like those of the other, it is just as likely for one stock as the other to have yielded the pollen used for the cross.

But it would be a thankless task to attempt to correct all the hasty, careless, and erroneous statements, past and present, and it will probably be of greater utility to give a general survey of what has been ascertained concerning the form and temperament of hybrids by impartial observers who have taken into account all the concurrent circumstances, and have allowed for the sources of error incidental to the experiments.

The formation of a hybrid plant presupposes two stock-plants as parents which have different properties and characters. A cross must take place between the two —that is to say, the stigma of the one must be dusted with pollen from the other; the pollen must put forth pollen-tubes and an effectual union between spermatoplasm and ooplasm must be effected. For the sake of brevity, the plant from which the pollen, and therefore also the spermatoplasm, is derived is called the paternal stock or father-plant, and that which has its stigma dusted and its ooplasm fertilized is called the maternal stock or mother-plant. As a plant's external marks and characteristics, which are perceptible to our senses, are an expression of its internal organization and of the specific constitution of its protoplasm, it may be assumed that the plant-individual which owes its existence to the union of two protoplasts

of different constitutions possesses marks and attributes, some of which are characteristic of the father and others of the mother. As a matter of fact, the individuals which growers call by the various names of hybrids, mongrels, and bastards answer to this supposition. Some of their attributes and external characters are derived from the paternal, some from the maternal stock. If the relative admixture of the two stocks were to be determined in the case of a hybrid by summing up the characteristics transmitted from each source, the share of each parent would in many cases be found to be a half. In such a case it is usual to say that the hybrid is a mean between its parents. Examples are afforded by *Geum hybridum*, which originates from crossing *Geum montanum* and *G. rivale*, *Hieracium stoloniflorum*, derived from *Hieracium aurantiacum* and *H. pilosellæforme*, and *Nuphar intermedium*, a cross between *Nuphar luteum* and *N. pumilum*. But it also happens sometimes that the proportion of characters inherited by a hybrid from one of the parent-stocks amounts to about two-thirds, leaving only one-third as the proportion inherited from the other, and in that case the hybrid is said to exhibit an approximation to one of the parent-species. The Saxifrage hybrids are very instructive examples of this class. The stigmas in a flower of *Saxifraga aizoides* were dusted with the pollen of *S. cæsia*. Fertilization was successfully effected, and a capsule containing fertile seeds came to maturity. The plants reared from these seeds resembled in some cases the intermediate form described by Botanists under the name of *Saxifraga patens*; others approximated more closely to the paternal stock, and a third group to the maternal stock. A similar result was obtained by crossing a flower of *Saxifraga aizoides* with the pollen of *S. mutata*. From seeds of the same capsule were produced two different kinds of hybrid, of which one was intermediate between the parents (*Saxifraga Hausmanni*), whilst the other (*Saxifraga inclinata*) approximated more closely to *S. mutata*. These experiments point to the conclusion that the share which each parent has in the form of a hybrid depends upon the quantity of its spermatoplasm or ooplasm, as the case may be, used in the production of the seedling relatively to the quantity derived from the other parent; and in the case of hybrids issuing from the same fruit we are forced to suppose that the variability of the degree in which a particular form is inherited is caused by the existence of quantitative differences between the several spermatoplasmic and ooplasmic nuclei (or cells) which coalesce in pairs in the interior of the same ovary.

Important evidence in support of this supposition is derived from experiments made in connection with the crossing of various composites of the Thistle genus (*Cirsium*). In these plants each ovary contains a single ovule only, and therefore each fruit can only produce a single individual. On the other hand, each capitulum is composed of a large number of florets, and when a head is in full bloom nearly a hundred mature stigmas project from it in close proximity to one another. If pollen from another species is transferred by means of a paint-brush on to these stigmas, wholesale crossing, so to speak, ensues; and it may be confidently expected that a proportion of these simultaneous crosses will be effectual. The harvest of fruit

from the capitula selected for the experiment was not, it is true, very plentiful, but some fruits invariably came to maturity. If these one-seeded fruits, all of which have originated at the same time and under similar conditions, are sown, the individuals produced from them are but seldom like one another. The attributes and external marks of the paternal and maternal stocks respectively are in some represented in the proportion of about 2:1, in others in the proportion of 1:2, and in a third class in practically equal proportions; cases are even known where four, five, or more distinct forms of hybrid have developed from the fruits of a single capitulum. I found the most striking differences amongst the hybrids obtained by crossing a capitulum of *Cirsium oleraceum* with the pollen from a capitulum of *Cirsium heterophyllum*. Those produced by crossing a head of *Cirsium Pannonicum* with pollen from a head of *Cirsium Erisithales* were scarcely less conspicuously diverse. As it must be presumed that the spermatoplasm and ooplasm—or rather the spermatoplasmic and ooplasmic nuclei—which have been formed in the adjacent florets of a capitulum are alike in composition and ultimate structure, the variety of the hybrids springing from such florets must depend solely on the relation between the masses of ooplasm and spermatoplasm respectively which coalesce in a flower, and the ratio between these masses must be in the one case 1:2, in a second 1:1, and in a third 2:1. Of course these ratios give but an approximate measure of the degree in which each parent has participated in the generation of the intermediate forms. Where five kinds of intermediate forms occur the series would be approximately represented by the ratios 1:4, 2:3, 1:1, 3:2, and 4:1. The first time flowers of a head of *Cirsium Erisithales* were crossed with pollen from *Cirsium palustre* they produced two different forms of hybrid, one of which approximated to the paternal, the other to the maternal stock; but no form exactly midway between the two parent-stocks was obtained. A second trial of the same experiment resulted in the production of a single form which did occupy this intermediate position. These observations show that there is no definite law governing the form of hybrids; one might even say that irregularity is here the rule. On one occasion all the individuals which are the result of a cross between two species are alike, on another occasion they constitute more or less numerous links in a chain of intermediate forms.

Hybrids which do not stand midway between the parent-species but approximate to one or other of them are called *goneoclinic* (γονεύς=parent, κλίνω=I lean). That such hybrids may arise from a first cross is established beyond question by the experiments above recorded; but there is also another process whereby they are produced, and that is the crossing of a hybrid with one of its parent-stocks. These crosses are effected in great numbers, and all observers agree that in general the results are better in such cases than where two species are crossed; that is to say, if a hybrid's stigmas are dusted with the pollen of one of the parent-species a larger number of fertile seeds may be looked for than if the plants crossed were of distinct species. The individuals resulting from the cross of a hybrid with one of the parent-stocks also occupy, as might be expected, a position as regards marks and attributes

intermediate between their progenitors; here again, however, forms are not always alike, and sometimes several intermediate forms make their appearance. If the hybrid derived from *Cirsium Erisithales* and *C. Pannonicum*, which inherits equally from both parents, be crossed with pollen from *Cirsium Erisithales*, the resulting individuals have a stronger resemblance to the latter species and are instances of goneoclinic hybrids. But when *Cirsium Erisithales* and *C. Pannonicum* are crossed for a first time hybrids are also produced which are not exactly midway between the parents but are more like *C. Erisithales*. These naturally resemble the goneoclinic hybrid derived from crossing the offspring of *C. Erisithales* and *Pannonicum* with *C. Erisithales*, and if one were not in a position to follow the history of the origin of the hybrid in question its characteristics alone would not furnish sufficient data for a judgment as to the mode of production of the goneoclinic hybrid.

Hybrids which are the offspring indirectly of three different species are called ternary hybrids. The word "indirectly" must be specially emphasized here, lest the reader should fall into the error of supposing it to be possible that pollen-tubes from two or more species should simultaneously fertilize a single ovule. Such an occurrence never happens, not even if a mixture of pollen belonging to two or more different species be placed upon the stigma of a particular flower. On the other hand, it has been ascertained by numerous experiments that if the hybrid-offspring of two species is crossed with the pollen of a third species, or *vice versâ*, another hybrid is produced. Thus, for instance, if the hybrid of *Linaria genistifolia* and *L. purpurea* is crossed with the pollen of *L. striata* the result is a ternary hybrid. In one experiment the stigmas in a capitulum of *Cirsium Linkianum* (the hybrid offspring of *C. Erisithales* and *C. Pannonicum*) were dusted with pollen taken from *C. palustre*. A considerable number of fruits ripened, and the hybrids which arose from them were ternary hybrids, exhibiting marks and characteristics of *C. Erisithales*, *C. Pannonicum*, and *C. palustre* respectively. These hybrids, moreover, were not all alike; some of them bore striking resemblance to *Cirsium aquilonare*, the hybrid produced by crossing *C. palustre* and *C. Pannonicum*, and exhibited very few of the peculiarities of *C. Erisithales*, whilst other individuals were extremely like *Cirsium ochroleucum*, the hybrid obtained by crossing *C. Erisithales* and *C. palustre*, and only showed slight indications of its relation to *C. Pannonicum*. Growers of garden-flowers have achieved great success in producing ornamental ternary hybrids in a number of genera (*Achimenes*, *Begonia*, *Dianthus*, *Gladiolus*, &c.). Ternary hybrids of various Willows are also met with in gardens; one of these is obtained by crossing *Salix Cremsensis*, a hybrid of *Salix Caprea* and *S. daphnoides*, with *S. viminalis*, another by crossing *Salix Wichuræ* (the hybrid-product of *S. incana* and *S. purpurea*) with *S. cinerea*, and so forth. Willows have been also used for the prosecution of still further experiments. The crossing of two hybrids of different parentage on both sides resulted in the genesis of hybrids combining four species of Willow. Indeed, six different species of Willow have on one occasion been combined by successive crossing—Wichura having

succeeded in producing in Breslau a compound hybrid in which were united *Salix Caprea*, *S. daphnoides*, *S. Lapponum*, *S. purpurea*, *S. Silesiaca*, and *S. viminalis*.

It need hardly be said that the characteristics of the six ancestral species in such a case as that of the last-mentioned hybrid are not easily identified. Even where a hybrid is the offspring of a single cross between two species it is not always easy to determine its origin from its external appearance, and in the absence of any knowledge of the history of its production. The characteristics of the parent-stocks are not combined in all hybrids according to a single definite rule. Sometimes the combination seems to amount to a complete *fusion*, so that the form produced might be compared to an alloy of two metals. Very often a new form is generated which combines in a definite geometrical ratio the characteristics of the parents in respect of the position and direction as well as the shape and size of its separate parts. In that case there is said to be a union of the parental characters. The structural characters of both stocks are represented unmodified, but are so closely bound together as to suggest a composite crystal founded upon two different crystalline forms. Just as in definite combinations of crystals the faces of one component form are dominant, and determine the general aspect in one case and those of the other component form in another case, so in many hybrid plants sometimes the attributes of the one parent, sometimes those of the other, are most conspicuously reproduced. Other hybrids again are analogous to combinations in which both crystalline forms are equally represented. Again, in addition to the above classes of hybrids wherein the parental characters are either completely merged together or intimately united there are many cases where those characteristics are present almost unchanged, and subsist side by side like the particles of a rock. The most common case of this *mixture* or juxtaposition of properties occurs where the hybrid displays hairs, glands, or prickles of two forms interspersed together, one of which is identical with the form of the structure in question exhibited by the maternal stock, whilst the other has been inherited unchanged from the paternal stock. Or, one part of the hybrid's flower may be coloured like one parent and another like the other parent. Hybrids are also known in which the foliage is almost indistinguishable from that of one parental stock whilst the flowers are like those of the other, so that at first sight a hybrid of the kind looks as if it were a plant of the former species with flowers of the second species affixed to it for a joke. On closer inspection some slight differences may be perceived between the leaves and flowers of the hybrid and those of the parent species respectively, but this does not alter the fact that hybrids exist whose leaves resemble far more closely those of one parent, whilst their flowers are more like those of the other. Probably it was the occurrence of such a hybrid which suggested the proposition referred to on p. 557 that in the product of a cross between two species the flowers reveal the paternal and the foliage the maternal stock. But this statement is incorrect, as was said before, for some hybrids approximate to the maternal stock in respect of their flowers, and to the paternal stock in respect of their leaves.

Of the three ways in which the parental characters may be combined in a

hybrid—*i.e.* by fusion, by union, or by mixture—one alone sometimes prevails in all the parts; but usually, on the contrary, there is an incalculable degree of variation in this connection. There are, for example, Rose hybrids in which the outline of the leaves exhibits a union, the colour of the flowers a fusion, and the hairs a mixture of the corresponding characters in the parents.

A brief account will now be given of a few examples to illustrate the manner in which the combination of parental characters in a hybrid is manifested throughout the structure of the plant and particularly in the forms of the stems, leaves, and flowers, and in those of thorns, bristles, hairs, and other epidermal appendages. The species of Willow known as *Salix Caprea* grows in the form of a little tree, with thick, straight, erect branches, each of which bears about 25 leaves; *Salix repens*, on the other hand, is a low shrub with a procumbent stem and slender, rod-like branches ascending in curves from it, and each bearing about 40 leaves. The hybrid of these two is a small tree with a bent stem and ascending branches, which in length, thickness, curvature, and direction are intermediate between the *Salix Caprea* and *Salix repens*, and which are furnished with some 30 leaves apiece. Again, the foliage-leaves of *Prunella vulgaris* have their margins entire, whilst those of *P. laciniata* are deeply cut, and their hybrid *Prunella intermedia* has lobed leaves. The leaves of *Potentilla sterilis* (or *P. Fragariastrum*) possess three leaflets, each leaflet being furnished on either side with from four to five serrate indentations. The leaves of *Potentilla micrantha* likewise possess three leaflets, but each leaflet has from seven to ten serrate teeth on each side. In the hybrid of these two species the leaflets have from six to eight indentations on each side. The shape of the leaf is, as is well known, intimately connected with the course, ramification, and disposition of the bundles called nerves. Now, if the net-work of strands in the leaves of the parent-species is compared with that in the leaves of the hybrid, it is astonishing to find how the union of the two systems may be traced in the minutest details. No group of plants lends itself better to this sort of investigation than the Willows. Even if a single leaf of the hybrid offspring of two species of Willow is submitted for inspection, it is possible in most cases to determine, from the number and distribution of the nerves, the identities of both its parents. *Salix purpurea* produces one hybrid when crossed with *Salix grandifolia*, and a second when crossed with *Salix Caprea*. *Salix grandifolia* has twice as many lateral nerves in each leaf as *Salix Caprea*, and this difference is reproduced in the corresponding hybrids, whose leaves in all other respects resemble one another closely.

The involucral leaves of Composites are well known to be extremely diverse in shape, and systematic Botanists have always attributed great importance in the discrimination of species to the size, shape, and margination of these leaves and to the peculiar appendages at their apices. Now, the hybrids of Composites not infrequently have involucral leaves which differ widely from the forms characteristic of the parent-stocks. Thus, for instance, each leaf of the involucre in a capitulum of *Centaurea rupestris* terminates in a long yellow prickle, whilst the

corresponding structure in *Centaurea Scabiosa* is bordered by a broad, membranous, fringe-like edge of a dark-brown colour. In *Centaurea sordida* (*Grafiana*), the hybrid offspring of these two species, each involucral leaf is edged with a narrow, light-brown membranous and fringed border, and terminates in a short yellowish prickle. A very instructive example of the union of parental characters affecting all the different parts of the floral region is afforded also by the Labiate *Marrubium remotum*, which is produced by crossing *Marrubium peregrinum* and *M. vulgare*. The small tuft-like inflorescences in the leaf-axils of *Marrubium peregrinum* include from 10 to 18 flowers, those of *M. vulgare* from 4 to 5, and those of the hybrid *M. remotum* from 5 to 10. The calyx of *M. peregrinum* is grey and covered with felted hairs, and its margin is provided with five large subulate teeth which terminate in straight points. The calyx of *M. vulgare* is green and sparsely clothed with hairs, and its edge has ten small teeth which terminate in stiff reflexed points like hooks. Five of these teeth are rather longer than the rest. The calyx of *M. remotum* is greyish-green and clothed with a loose felt; its edge is furnished with five big subulate teeth which terminate in stiff out-curved points, and have from two to five very small teeth interspersed between them. The three lobes of the under-lip of the corolla are almost of equal length in *Marrubium peregrinum*, whilst in *M. vulgare* the middle lobe is three times as long as the two lateral lobes. In the hybrid *Marrubium remotum* the middle lobe of the lower lip is half as long again as the lateral lobes. An excellent example is also afforded by *Dianthus Œnipontanus*, a hybrid Pink resulting from a cross between *Dianthus alpinus* and *D. superbus*. In *D. alpinus* the bract-like scales at the base of the calyx are almost as long as the tube of the calyx itself, whilst in *D. superbus* their relative length is only a quarter or a third; in the hybrid *D. Œnipontanus* these bracts are half as long as the tube. The petals of *D. alpinus* have broad laminæ beset at the margin with short triangular teeth, those of *D. superbus* have their laminæ slit up into a number of narrow strips, and those of *D. Œnipontanus* have deeply-incised laminæ, the margins being divided into linear segments. The dimensions of the various parts of the flower in a hybrid also exhibit in most cases a combination of the corresponding parental characteristics. Thus, for instance, the perianth of the Orchid *Gymnadenia conopsea* has a long spur—that is to say, the segment of the perianth known as the labellum is produced backwards into a saccate protuberance supposed to resemble a spur, and this portion of the petal in *Gymnadenia conopsea* is 15 mm. in length. In *Nigritella nigra*, on the other hand, the spur is very short, measuring about 2 mm. The hybrid of these two Orchids, *Nigritella suaveolens*, has a spur varying from 5 to 7 mm. in length. In Willow hybrids the number of stamens in each flower of the hybrid is invariably between the corresponding numbers in the two parent-species. For example, the number of stamens in a flower of *Salix alba* is 2, in *Salix pentandra* 5–12, and in their hybrid *Salix Ehrhartiana* 3–4.

The cellular structures produced from the epidermis of the stem and leaves which are differentiated as hairs, bristles, scales, glands, &c., and are classed together

under the name of investments (*indumentum*), are very constant characters in most species of plants. The occurrence of stellate hairs, in particular, is looked upon by systematic Botanists as an important point in assisting them to distinguish between similar species, and so also is the presence of glandular hairs composed of simple rows of cells, and terminating in globular bladders full of ethereal oils. Hybrids exhibit the most varied combinations of the indumenta of their parents. In the majority of cases the characteristics of the two stocks in this respect are mixed, but less frequently are they united, and in the latter case the shape, size, and number of hairs, bristles, scales, and glands are intermediate between those of the same appendages in the two parent-species. The Lungwort genus (*Pulmonaria*), which has a special tendency to hybridization, includes only a few species, but each one may be recognized by the nature of its indumentum. Thus, *Pulmonaria officinalis* is distinguished by the thousands of short unicellular prickly hairs, scarcely perceptible to the naked eye, which are interspersed amongst the long scattered bristles on the upper surfaces of the leaves. In *Pulmonaria angustifolia* the leaves are destitute of these minute prickles, but bear on their upper surface a more abundant quantity of straight appressed bristles of equal length. The leaves of the hybrid derived from the two preceding species, viz. *Pulmonaria hybrida*, are richly supplied with long bristles, and interspersed amongst these may be seen a large number of shorter bristles which are about two or three times as long as the prickly hairs of *Pulmonaria officinalis*. A very instructive example is also afforded by the hybrid *Rhododendron intermedium*, which is easily produced by crossing the two Alpine-Roses (*Rhododendron ferrugineum* and *Rhododendron hirsutum*). The upper faces of the leaves of *R. ferrugineum* are dark-green, smooth, and shining, whilst their backs are rusty and dull owing to the presence of a dense crowd of tiny scales. The margins are not ciliate. The leaves of *R. hirsutum* are light-green and beset with scattered whitish glands (see vol. i. p. 232, figs. 54^5 and 54^6), and their margins are fringed with long hairs. In *Rhododendron intermedium* both kinds of epidermal appendage are displayed side by side. The under surface of the leaf is furnished with brown scales, though not so profusely as in *Rhododendron ferrugineum*, and its edge is fringed with hairs, but not so thickly as in *R. hirsutum*. The same sort of thing occurs in Roses, Cinquefoils, Blackberries, Drabas, Hawkweeds, and many other plants. Where one parent Rose bears only non-glandular and the other only glandular hairs the hybrid is sure to be clothed with a mixture of the two kinds of hairs. Several species of Cinquefoil (*Potentilla*) have stellate or tufted hairs, whilst others are entirely free from them and bear none but simple hairs on their leaves. In hybrids derived from two of these species—one with compound and the other with simple hairs—stellate or fasciculated hairs are invariably intermixed with a large number of simple hairs. A few species of the perennial Whitlow-grasses (*Draba*), which are indigenous to mountainous districts in Central Europe, have rectilinear anvil-shaped hairs, whilst others have three- or four-rayed stellate hairs. In the hybrids which spring from these different species rectilinear and stellate hairs grow together on the same leaf. If the hairs of two parent-species are of the

same form but of unequal length, those of their hybrid offspring have a length which corresponds approximately to the mean between the lengths in the parent-species. Thus the length of the hairs on the backs of the leaves is 0·3 mm. in *Salix aurita*, 1·2 mm. in *Salix repens*, and 0·6 mm. in their hybrid *Salix plicata*. The hairs in *Salix Caprea* measure 0·8 mm., in *Salix viminalis* 0·3 mm., and in *Salix acuminata*, their offspring, 0·5 mm. Whenever one stock is glabrous and the other hairy, one may be quite sure that the corresponding parts of their hybrid will be furnished with hairs, but less profusely than the parent-species from which that particular characteristic is derived. This is the case, for instance, with *Primula Sturii*, the hybrid produced by crossing the glabrous *Primula minima* with *Primula villosa*, which has glandular hairs. The leaves of the latter are thickly covered with these hairs, which vary from 0·7 mm. to 1 mm. in length, and *Primula Sturii* has scattered glandular hairs which measure 0·3 mm. The hybrids obtained by crossing the Purple Willow (*Salix purpurea*) with the Common Osier (*Salix viminalis*) are distinguished by Botanists into two sections, one of which—*Salix rubra*—approximates to the Purple Willow and the other—*Salix elæagnifolia*—to the Common Osier. The leaves of the Purple Willow when mature are glabrous at the back, those of the Common Osier have small glistening hairs lying appressed to their under surfaces, parallel to the lateral nerves, and measuring 0·3 mm. There are about 1800 of these hairs on a square millimetre. The hairs of the hybrid *Salix elæagnifolia* are of the same length as those of *S. viminalis*, but there are only about 800 of them to the square millimetre, whilst the hairs of the hybrid *Salix rubra* are somewhat shorter, and there are only 400 to the square millimetre.

Recently the discovery has been made by Wettstein that the form and disposition of the cells and tissues in hybrids is also a combination of the corresponding characteristics in the parent-species. The various species of the Pine genus (*Pinus*) may be distinguished with certainty by the anatomical structure of their needle-shaped leaves, in particular by the thickness of the epidermal cells, the number of the stone-cells lying beneath the epidermis, and the number of the resin-ducts. In the hybrids the anatomical characters of the parents in these respects are united, and the result is indeed often an exact arithmetic mean between the two. Thus a needle of the Scotch Pine (*Pinus sylvestris*) contains from 6 to 10 resin-ducts, that of the Mountain Pine, *Pinus Mughus* (*montana*), contains from 3 to 5, and that of the hybrid offspring of the two from 5 to 7 such ducts. The Junipers (*Juniperus*) afford a similar instance. In their case the leaves are distinguished by the various thickness and length of the layer of sclerotic-cells which covers the back of each leaf, by the width of the resin-duct running through the middle of the leaf, and by the number of the cells encasing that duct. In the hybrids, such as *Juniperus Kanitzii*, which is produced by crossing *Juniperus communis* and *J. sabinoides*, there is evidently a union of the parental attributes in the corresponding cellular structures in the leaves. It has also been shown by Hildebrand that in the Wood-Sorrel (*Oxalis*) hybrids also the anatomical characters of the parents are united, but by far the most comprehensive study which has

been made in recent times into the minute structure of plant-hybrids is by Macfarlane. He selected a number of hybrids, and worked through their anatomy from base to apex in the most painstaking manner. He dealt with roots, stems, leaves, and the various portions of the flower, always comparing their various tissues (both as regards size, form, and distribution) with those of their parent-forms. And his result is to confirm what has been written above, though it is obvious he had never read these pages. Amongst the more interesting of his results may be mentioned those on starch-grains. Of course in a great many of the parent-forms uniting to form a hybrid there is no recognizable difference in the size or structure of the starch-grains. But in the genus *Hedychium* (belonging to the family Zingiberaceæ) exceptions to this rule were found. Thus, those of *Hedychium Sadlerianum* are intermediate in form and size between those of its two parents, *H. Gardnerianum* and *H. coronarium*; and those of a hybrid between *H. elatum* and *H. coronarium* exhibited similar intermediate characters.

It is important to note also that the aromatic substances and colouring matters produced in the cells of a hybrid are inherited partly from the maternal, and partly from the paternal stock. As we have several times already had occasion to mention, the various species of the Rose genus may be recognized at once by their peculiar scent. The perfume of *Rosa Centifolia* is the one which in particular is understood by the rose-scent, but it is very different from that of *Rosa alpina*, and the latter in its turn is unlike any of the scents emitted by *Rosa arvensis*, *R. Gallica*, *R. Indica*, &c. *Rosa Nasterana* has a scent strongly resembling that of Pinks, whilst *Rosa lutea* and *R. punica* are notorious for their disagreeable smell. Now the hybrid Roses emit odours in which the scents of the parent-species are merged together in a great variety of ways. Usually the scent of one stock predominates, and there is only a suggestion of the other. Sometimes, however, an entirely new scent is evolved from the fusion of the two, as is the case, for instance (according to Macfarlane), in *Hedychium Sadlerianum*, the hybrid between *H. Gardnerianum* and *H. coronarium*; and, again, in other cases, one of the component odours is intensified and the other is extinguished. The same statement applies to the aromatic substances to which the scent of the foliage is due. The hybrids of *Rosa glutinosa*, *Rosa rubiginosa*, and *R. rugosa*, with *Rosa Gallica* and *R. Centifolia*, are very interesting in this connection. The aromatic substances which are contained in fruits and excite our nerves of taste are also inherited, partly from the maternal and partly from the paternal stock. Owing, however, to the difficulty of naming the various sensations of smell and taste it is of little use to discuss the subject more fully.

As regards the colouring-matters reproduced in hybrids the first point to notice is that in cases where the foliage is of different shades of green in the parent-species the leaves of the hybrid exhibit a shade intermediate between the two. Conspicuous instances of this are afforded by the hybrid Willows derived from *Salix nigricans* and *S. purpurea*. In both these species the foliage becomes *black* when it withers, and this characteristic is transmitted, though not in its full strength, to the hybrids

which *S. nigricans* and *S. purpurea* form with other Willows whose foliage turns *brown* when it dries up. The colour of the flowers in hybrids is usually the result of a *fusion* of the colours in the parent-species; less frequently it is a *mixture* of the original colours. The cases of fusion occur especially amongst the hybrids of Orchids, Louseworts, Anemones, Pulsatillas, Medicagos, and Mulleins. If the tone of the red or blue petals in one parent-species is dull and in the other bright, the same colour reappears in the hybrid, but of a medium tone. Thus the colour of the petals in *Gymnadenia conopsea* is rose-red and in *Nigritella nigra* dark blood-red, whilst in their hybrid, *Nigritella suaveolens*, it is bright carmine. The corolla of *Pedicularis incarnata* is of a subdued carmine tint, and that of *P. recutita* of a dark reddish-brown, whilst their hybrid, *P. atrorubens*, has a dark purple corolla. Where the floral colour of one parent-species is white and that of the other a full yellow, red, or blue, the hybrid's flower usually exhibits a pale yellow, red, or blue coloration. The flowers of *Anemone nemorosa* are white, those of *A. ranunculoides* golden-yellow, and those of their hybrid, *A. intermedia*, sulphur-yellow. The colour of the flowers in a hybrid whose parents have yellow and violet, or blue flowers, respectively, is very remarkable. *Medicago media*, which is the hybrid offspring of the yellow-flowered *Medicago falcata*, and the blue-purple flowered *M. sativa* very often has green corollas. The hybrids (*Verbascum commutatum*, *V. rubiginosum*, *V. Schmidtii*, *V. versiflorum*, &c.) obtained by crossing the yellow-flowered Mulleins with *Verbascum phœniceum*, whose flowers are a conspicuous purple, all display a bright brown tint in their corollas. The colour in question is just the same as that which is produced by mixing gamboge with the purple prepared from carmine and indigo. Quite a different tint is exhibited by the corolla of *Verbascum pseudophœniceum*, the hybrid generated by crossing *V. Blattaria* and *V. phœniceum*. One of the parent-species (*V. Blattaria*) in this case has pale yellow and the other (*V. phœniceum*) violet-purple corollas, and in the hybrid (*V. pseudophœniceum*) the corolla is pale crimson. Nor are cases wanting in which hybrids have been produced from forms with red and blue flowers respectively. The brilliant scarlet-flowered *Delphinium nudicaule* has been crossed in the Edinburgh Botanic Garden with the dark blue-flowered *D. cashmirianum*, the hybrid product being of a lurid purple-red hue. Darwin obtained by crossing the red and blue Pimpernels (*Anagallis*) a progeny some of which were blue, some red, and some intermediate in colour. As a final instance of this colour-fusion may be cited the hybrid Pitcher-plant *Nepenthes Mastersiana*. This hybrid is produced from *N. sanguinea*, the pitchers of which are of large size and vary in colour from greenish-scarlet to crimson, and of *N. Kharsiana*, which bears long narrow pitchers, varying from yellowish-green to dull red-green. The hybrid (says Macfarlane) presents a corresponding latitude in colour effect, though on the average it is greenish-crimson.

The hybrids which originate from crosses between *Primula Auricula*, whose flower is all of one colour, and *Primula Carniolica*, *P. hirsuta*, *P. Oenensis*, *P. villosa*, &c., which have bi-coloured flowers, are also of great interest in this connection. *P. pubescens*, the hybrid produced by crossing *P. Auricula* and *P. hirsuta*,

is the stock from which the garden Auriculas are derived. The colour of the corolla in *P. Auricula* is a uniform golden-yellow excepting that at the throat, i.e. at the junction of the tube with the expanded limb, there is a floury efflorescence which, like that covering the calyx, pedicels, and bracts, is due to a peculiar modification of the epidermis. The corolla of *P. hirsuta* is bi-coloured; the segments of the limb are violet-red, whilst the throat is white. The two tints are sharply marked off from one another, and in consequence a white five-rayed star is seen in the middle of the flower. There is in this case no trace of a floury efflorescence. In the hybrid offspring of these two Primulas both the violet-red of the limb and the white of the throat are blended with yellow; the former exhibits a touch of brown, and in the middle of the flower is a pale-yellow star.

It is much less common for those floral colours which are inherited by a hybrid from the parent-species to be displayed in juxtaposition than in a blended condition. Since the time of the Roman Empire gardeners have crossed the red-flowered *Rosa Gallica* and *R. Damascena* with the white-flowered *Rosa alba* and obtained thereby hybrids in which the petals are striped and spotted longitudinally with red and white (so-called "York and Lancaster" roses). Similar cases occur amongst hybrid Calceolarias, Pinks, Petunias, and Wood-Sorrels, and instances of Tulip and Iris hybrids are also known where the perianths exhibit the two different colours of the parent-species side by side in streaks and patches. A hybrid of *Iris Florentina* and *I. Kochii* is especially deserving of notice. The perianth in *I. Florentina* is milk-white and that of *I. Kochii* is dark violet. The hybrid of these two species was first obtained in May, 1871, in the Botanic Garden at Innsbruck; one of the individual plants thus produced had two of the outer and one of the inner members of the perianth shaped like those of *I. Kochii* and of a deep violet colour, and one of the outer and two of the inner members shaped like those of *I. Florentina* and milky-white in colour. This arrangement of colours re-appeared year after year until in 1877 a single flower, in which the lower white members had some dark violet streaks widening out from the middle to the edge of the perianth also made its appearance. A second plant of the same hybrid developed flowers which only differed from those of *I. Florentina* in that a few of the white petals had dark violet streaks widening out towards the circumference. An equally noteworthy case is that of a hybrid reared in the Botanic Garden at Florence from *I. Germanica* and *I. sambucina*, of which a specimen was sent to me in 1872. One inferior and two superior perianth-members displayed on one half of their surfaces the colour and pattern peculiar to *I. sambucina*, and on the other half those characteristic of *I. Germanica*. The rest of the perianth could not be distinguished except by its smaller size from that of *Iris Germanica*.

It must not be supposed, however, that the presence of variegated stripes, patches, or speckles on petals is always an indication of hybridity. *Viola polychroma*, a very common Alpine species, not infrequently produces simultaneously two, three, or four open flowers, every one of which presents a different mixture of tints, and amongst plants of this species covering only a small patch of ground it

would be easy to find 100 blossoms with corollas differing from one another in the distribution of their colours and in the arrangements of the spots and streaks upon them. Similar phenomena are exhibited by *Iris pumila* and *Polygala amarella*. The flowers in *Polygala amarella* are equally blue and white or sprinkled with blue and white, and it is also no rare thing for plants to bear white flowers interspersed with a few which are sprinkled with blue. In the same way several species of *Anthyllis*, *Euphrasia*, *Galeopsis*, *Linaria*, *Melittis*, *Ophrys*, *Orchis*, *Saxifraga*, &c., exhibit considerable variation in the colours and markings of their petals, which yet is not to be attributed either to hybridization or to the influence of soil or climate. Reference must also be made here to the large number of species (already mentioned on p. 194) in which the floral coloration is by turns blue and white, red and white, blue and red, yellow and white, and so on. Heterochromatism, *i.e.* the change in the coloration and marking of petals, serves, in fact, in some plants as a specific character. Contrasting with these heterochromatic species are those with homochromatic flowers, which, as far as experience has shown, invariably present the same colour and pattern, and only exhibit a slight variation in the depth of the colour when subjected to the influence of light of varying degrees of intensity. *Iris Kochii* and *I. Florentina*, *Primula Auricula*, and *P. hirsuta*, together with other pairs of species referred to above as the progenitors of hybrids of special interest, belong to the category of plants possessing homochromatic flowers, and it is obvious that in the hybrid offspring of such plants the floral coloration would be an important sign of identity.

This will be the most convenient place in which to introduce a few words concerning the *Bizzaria* of Italian gardeners, and also concerning so-called *graft-hybrids*. The name of *Bizzaria* has been given by the Italians to an extremely curious Orange. Gallesio (1839) states that this Orange-tree produces at the same time foliage, flowers, and fruit identical with the Bitter Orange (*Citrus Aurantium*) and with the Citron of Florence (*Citrus medica*), and likewise compound fruit, with the two kinds either blended together, both externally and internally, or segregated in various ways. In the fruits of the *Bizzaria* which I have seen, five longitudinal stripes of the colour of a Citron were interpolated in the fruit of the Orange. Other fruits were, on the whole, like Oranges, excepting as regarded an eighth of their mass, which in form, colour, and taste resembled a Citron, and was also peculiar for its extreme convexity. This anomalous segment stretched in the form of a light-coloured cushion from one pole of the spherical fruit to the other. Growers maintain that the *Bizzaria* is the result of a cross between *Citrus medica* and *Citrus Aurantium*, though the gardener who, in 1644, in Florence, raised this tree, declared it was a seedling which had been grafted, and after the graft had perished the stock sprouted and produced the *Bizzaria* (according to which account it would be a graft-hybrid). In other similar cases of *Citrus* hybrids, however, such as the Bergamot Orange, alleged to be a hybrid of the ordinary Lemon and the Bitter Orange, one finds the characteristics of the parent-species do not

reappear in juxtaposition (as in the *Bizzaria*), but are united or fused together. Whether the case of Bergamot Pears, which are striped green and yellow, and that of the half dark- and half light-coloured grapes, of which a few occur occasionally in otherwise ordinary bunches of the fruit, are to be looked upon as parallel phenomena to that of the *Bizzaria* must remain uncertain until it has been ascertained to what particular crosses of the various species of *Pyrus* and *Vitis* the innumerable Pear-trees and Vines now cultivated owe their origin.

Over and over again gardeners have asserted that hybrids may also be produced by budding and grafting, and in order to distinguish plants so arising from those which are the result of a cross (*i.e.* from true hybrids), they are called *graft-hybrids*. One of these plants, a Laburnum named *Cytisus Adami*, which exhibits a curious mixture of the characteristics of *Cytisus Laburnum* (the ordinary yellow Laburnum) and *Cytisus purpureus* in the same individual, has been the subject of lively discussion in scientific circles. It is indeed difficult to imagine anything more curious than a plant of *Cytisus Adami*. Most of the flowers derive their characters equally from both parent-forms; the calyx is not so thickly clad with silky hairs as in *C. Laburnum* nor so smooth as in *C. purpureus*, and the corollas are of a dirty-red colour, compounded of the purple of *C. purpureus* and the yellow of *C. Laburnum*. But the curious thing is that on many of the racemes a few blossoms of different appearance are interspersed amongst these red flowers, some having yellow corollas and silky-haired calices as in *C. Laburnum*, and others, still more remarkable, having half their petals like *C. purpureus* and half like *C. Laburnum*, or a third of their petals like *C. purpureus* and two-thirds like *C. Laburnum*, or some one of many other combinations. According to Schnittspahns, this anomalous form of *Cytisus* was first produced at Vitry, near Paris, in the year 1826, by a grower named Adam, who inserted a bud of *C. purpureus* into a stock of *C. Laburnum*. The shoot which sprang from the bud was not a pure branch of *C. purpureus*, but had characteristics derived both from *C. purpureus* and from *C. Laburnum*. Buds for propagating *C. Adami* were sent from Vitry to gardens all over Europe, and were in some cases inserted into stocks of *C. Laburnum*, and in other cases into stocks of *C. Jacquinianus* and *C. alpinus*. In many cases gardeners grafted buds of *C. purpureus* in addition to those of *C. Adami* on to the same stocks, and thus produced shrubs of most extraordinary appearance. Of the branches some resembled *C. Laburnum*, *C. Jacquinianus*, or *C. alpinus*, others *Cytisus Adami*, and others again *C. purpureus*; and amongst the racemes were many which bore the ordinary flowers of *C. Adami*, interspersed with a few blossoms of *C. Laburnum*, and others in whose flowers a mixture of the properties of *C. Laburnum* and *C. purpureus* was apparent. The fact of main interest, however, is that cuttings from Adam's original plant (the alleged graft-hybrid of *C. Laburnum* and *C. purpureus*) should bear not only flowers of an intermediate type (as might be looked for in a hybrid), but that on certain branches the flowers break back (or revert) to the pure form of one or other of the parents, or that a single flower should exhibit on one half the characters of one parent and

on the other those of the other parent. Thus the alleged graft-hybrid bears three distinct sorts of flowers, and often parti-coloured combinations of the two parent forms. The anatomical details of the tissues of the *Adami*-forms have been examined and compared with those of the two parent-forms by Macfarlane. It appears that the tissues show a remarkable mingling of the two parent-forms. In some the one, in others the other parent-form predominates. Though in the flowers (*i.e.* the pure *Adami*-flowers) the mingling is quite consistent with its being a well-balanced seed-hybrid, in the vegetative regions the strikingly diversified intermixture of tissues is unlike that met with in any seed-hybrid hitherto examined. It should be mentioned that where the *Adami*-plant bears *Laburnum* or *purpureus* shoots and flowers the anatomical characters of these shoots is identical with the normal *C. Laburnum* and *C. purpureus*, respectively. Finally the *Adami*-flowers never ripen seeds (the ovules being malformed), though when the parent-forms occur upon it they ripen fruit and seed.

As a general rule the relations of the graft to the substratum (or stock) are very different from those manifested in the case of Adam's experiment. The shoot developed from the ingrafted bud makes the same use of the substratum in which it is imbedded as a parasite makes of its host-plant (see vol. i. p. 213). It procures from the substratum a supply of "crude sap", and this material is absorbed and worked up by the protoplasts of the cells of the graft in the same way as the liquid substances of the soil which are sucked up by roots. It must be premised that those cells of the graft which take up the crude nutrient sap are adapted to their work in very much the same way as are the suction-cells of roots, that is to say, they are able to exercise a selective power, and only admit such substances as are good for the species to which the scion belongs. Any influence that the substratum might have on the graft could scarcely be other than such as would be exercised by soils of various composition. At the most we should expect variations in shape and colour, which have no permanence, and are not retained by the scion's posterity. As a matter of fact, if, for instance, cuttings are taken from an Apricot-tree and grafted on to various other Amygdaleæ, or are transferred from a Pear-tree to Quinces, White-thorns, and other Pomaceæ, they do not exhibit the slightest alteration in fruit, flowers, or foliage after entering into organic union with the stock. Again, when hybrid Roses produced by crossing are propagated by budding and grafting, the result is the same whatever species of Wild-rose is taken for the substratum or stock. In all the thousands of cases of propagation by these means none has been observed in which the stock has had any essential influence upon the form of the scion.

In 1876 and 1877 certain experiments were made in the Botanic Garden at Innsbruck on the genus *Iris*. They were suggested by the fact of the production of the hybrids of that genus already referred to, and consisted in grafting buds from the root-stock of one species of *Iris* on to that of another species of the same genus. The experiment was attended with perfect success, but the shoots and flowers developed from the ingrafted buds showed no trace of any influence on the

part of the substratum. Buds of *Iris Kochii* grafted on *I. Florentina* produced unaltered plants of *I. Kochii*, and buds of *I. Florentina* grafted on *I. Kochii* developed simply plants of *I. Florentina*. In the Botanical Garden at Vienna there is a male Ginkgo-tree (*Ginkgo biloba*) which, more than a hundred years ago, was the subject of an important experiment. When the tree was still quite small the bud of a female tree was grafted upon it by Jacquin, and a lateral branch was developed from this bud. What we have now is a mighty tree with a number of branches bearing male flowers, and one large branch bearing female flowers. The notable thing about the tree is that the grafted branch follows a course of development which is obviously different from that of the stock. Every year in the spring it puts forth foliage about fourteen days later than the male branches, and in the autumn its leaves are still green long after the rest have turned yellow and, for the most part, fallen off. From this instance we may infer that the shoots developed from the grafted bud adhere with the greatest tenacity even to individual characteristics, and do not suffer the substratum to affect them even in respect of their annual development.

These facts have of recent years led many people to the opinion that the genesis of graft-hybrids is simply a gardener's story, and that even the most famous of the supposed graft-hybrids—*Cytisus Adami*—does not owe its origin to budding, but to a cross between *Cytisus Laburnum* and *C. purpureus*. Still, in view of the curious mixing of the parent-characters in *Cytisus Adami*, as revealed by Macfarlane's investigations, it would perhaps be well to suspend our judgment. It is true that even in true seed-hybrids (*e.g.* the *Iris* hybrids mentioned on p. 568) a mixing (not a fusion) of the parental characters of the flowers was observed. Fresh observations in this field are wanted, directed especially with a view to showing whether or not the sum-total of the characters of *Cytisus Adami* are absolutely unique amongst hybrid-plants of whatsoever origin.

A further instance of the same nature may be mentioned, as it has been the subject of careful scientific investigation and experiment. In 1876 a Jerusalem Artichoke (*Helianthus tuberosus*) was grafted upon a Sunflower (*Helianthus annuus*) in the neighbourhood of Bristol, and it was alleged that as a consequence the Sunflower stock had acquired from the Artichoke the property of producing tubers on its subterranean portions. Quite lately a series of buds of the Artichoke were grafted on Sunflower stalks by Vöchting, and the results carefully followed. It was not found that the properties of the one were in any instance transmitted to the other, although scion and stock grew together in perfect harmony.

The importance of this subject is so great that I cannot refrain from trespassing for a moment on the domain of Zoology in order to refer to a case which shows that the animal world also sometimes affords instances of the characteristics of both parents being manifested in juxtaposition in their hybrid-offspring instead of being merged together or united in close combination. *Tetrao medius* is well known to be a hybrid produced by a crossing between the Black grouse (*Tetrao tetrix*) and the Capercailzie (*Tetrao Urogallus*). This hybrid is so common in Tyrol that the

poulterers in Innsbruck receive for sale on an average six specimens every year from huntsmen in the immediate neighbourhood. The plumage of some individual examples of *Tetrao medius* is curiously striped with alternate groups of feathers inherited from *T. tetrix* and *T. Urogallus* respectively. In 1879 a huntsman brought me from the remotest part of the Gschnitzthal in Tyrol a hen of *Tetrao medius* whose plumage exhibited a mixture of the feathers of *T. tetrix* and *T. Urogallus*, irregularly distributed in stripes and patches all over the body. The case of this hybrid affords valuable confirmation of the results of the experiments made on *Iris* hybrids, and there can no longer be any doubt of the fact that there are hybrids generated by crossing in which the parental characters reappear in juxtaposition.

In spite of all this, however, I should not like to deny the possibility of the existence of *graft-hybrids*, for there are certain considerations which tend to a contrary conclusion. In most cases the relation to the substratum of those cells of the ingrafted shoot or bud which take the crude nutrient sap from the stem of the stock-plant is just the same as that of a parasite's suckers; they are clearly marked off from the cells of the substratum and are not influenced thereby either in their shape or in their ultimate structure, whilst, conversely, no essential modification is undergone by the substratum through the presence of the graft. There is nothing, however, to exclude the possibility of a fusion between the protoplasmic contents of adjacent cells taking place at the spot where stock and graft unite, and the consequent development of a tissue which is composed of cells arising from a division of the cells containing the mixed protoplasms, and which unites the characteristic features of the tissues belonging to the stock and to the graft respectively. In fact, something of the kind has been observed in the case of the parasitic Balanophoreæ (see vol. i. p. 194). Now supposing such an intermediate tissue were to be formed at the junction between a graft and its substratum, one or more shoots might spring from it and they would doubtless combine the characteristics of the two species employed as stock and scion.

In relation to the genesis of new forms of plants in nature, the question of the possibility of the existence of graft-hybrids is of secondary importance; but it is of no small moment in connection with the comprehension of the processes involved in hybridization; for, the researches suggested by this problem have led to the conclusion that the marks and attributes of a particular species which are perceptible to our senses are an outward sign corresponding to the ultimate structure and molecular composition of a specific protoplasm, and that wherever the special characters of two species are united in a single plant-form, that form is built up from protoplasm which owes its origin to a combination of the protoplasms of two parent-species.

It is only by adhering to this train of thought that one is able to understand how it is that, also in the matter of chronological development, the vital manifestation connected with the shape, anatomical structure, scent, and colour occupy in hybrids a position intermediate between the corresponding manifestations in the parental species. In the Botanic Garden at Vienna there has been for many years

a Buckthorn-shrub, named *Rhamnus hybrida*, which sprang from a cross between *Rhamnus alpina* and *Rhamnus Alaternus*. One of the parent-species, *R. alpina*, has deciduous foliage, *i.e.* leaves which are green in the summer and wither and drop in the autumn; the other, *R. Alaternus*, has evergreen leaves, which last through the winter and remain on the branches for two years. The hybrid, *R. hybrida*, possesses leaves which do not fall off in the autumn, nor yet last fresh and green for two years, but which maintain their verdure through one winter and fall in the spring when new shoots are sprouting from the buds. The behaviour of hybrids as regards their season of flowering is also very remarkable. From 1863 to 1874 I kept notes concerning the flowering of some fifty different kinds of Willow, growing in the Botanic Garden at Innsbruck, and each year made an entry of the day on which the first flower opened in each plant, whether a pure species or a hybrid.

EARLIEST DATE OF FLOWERING OF A NUMBER OF WILLOWS GROWING IN THE BOTANIC GARDEN AT INNSBRUCK.

(The date given is the average for 12 years.)

Salix	Cremsensis -	March 17	Salix	Caprea - -	March 16	Salix	daphnoides	March 18
„	Mauternesis	„ 23	„	Caprea - -	„ 16	„	purpurea -	April 7
„	attenuata -	„ 25	„	Caprea - -	„ 16	„	grandifolia -	March 27
„	Wimmeri -	„ 26	„	daphnoides	„ 18	„	incana - -	April 17
„	Austriaca -	April 3	„	grandifolia -	„ 27	„	purpurea -	„ 7
„	Seringeana -	„ 3	„	Caprea - -	„ 16	„	incana - -	„ 17
„	capnoides -	„ 5	„	cinerea - -	April 10	„	incana - -	„ 17
„	intermedia -	„ 6	„	grandifolia -	March 27	„	incana - -	„ 17
„	rubra - - -	„ 6	„	viminalis -	April 3	„	purpurea -	„ 7
„	Kerneri - -	„ 10	„	viminalis -	„ 3	„	incana - -	„ 17
„	Oenipontana	„ 12	„	purpurea -	„ 7	„	incana - -	„ 17
„	auritoides -	„ 14	„	purpurea -	„ 7	„	aurita - -	„ 19
„	Fenzliana -	„ 21	„	retusa - -	„ 21	„	glabra - -	„ 21
„	retusoides -	„ 21	„	retusa - -	„ 21	„	Jacquiniana	„ 21
„	alpigena - -	„ 23	„	retusa - -	„ 21	„	hastata - -	„ 27
„	excelsior - -	„ 23	„	fragilis - -	„ 13	„	alba - - -	„ 27
„	Ehrhartiana	„ 29	„	alba - - -	„ 27	„	pentandra -	May 6

The name in the first column is that of a hybrid in each case, and the names on the same line in the second and third columns are those of its parent-stocks.

The above table, which gives the means of the dates recorded in 12 years of the first opening of the male flowers in 15 species and 17 hybrids produced from them by a variety of crosses, shows that the hybrids invariably flower on days between those on which the parent-species enter upon that stage of development. It will be observed that the two alpine Willows, *Salix retusa* and *Salix Jacquiniana*, flowered on an average in the 12 years on the same day, and that their hybrid *Salix retusoides* kept also to that date.

We have hitherto dealt with those of the marks, attributes, and vital phenomena manifested by hybrids which are derived partly from the one parent-species and partly from the other, and we must now pass to the consideration of such characteristics as cannot be attributed to inheritance from those species. There is, in the first place, the fact that the majority of the hybrids produced from crosses develop

with striking rapidity and exuberance; they not uncommonly flower the very first year after they are sown, whereas the seedlings of the parent-species may not attain to the flowering stage for two or three years; and in respect of the size of the foliage, and still more that of the flowers, hybrids often exceed both parent-species. The latter circumstance is indeed one of the chief reasons why growers make such frequent use of the process of crossing. They are thus enabled to meet the demands of connoisseurs, who prefer to have plants with conspicuous flowers in their gardens. The augmentation in the size of the flowers usually ceases after the first, or at any rate after the second year. Subsequently, the flowers of hybrids become smaller again. On this account gardeners are in the habit of producing such hybrids as are especially valued for their large flowers over and over again by the original method. Of the large number of observations recorded on this subject we will here mention one as an example. *Isoloma Decaisneanum* of the order Gesneraceæ is the product of a cross between *Isoloma Tydæum* and *Isoloma sciadocalyx*. The seeds obtained after crossing germinate early, and the seedlings develop rapidly into exceptionally robust plants. The foliage-leaves are three times as large and the flowers twice as large as those of the parent-species; in addition, the flowers are much more numerous than on the parent-plants, and in consequence the hybrid has a much more imposing and showy appearance than either of its progenitors.

Many plants which grow on soil rich in humus in mountainous regions, such as the Lungworts (*Pulmonaria*) and Primulas (*Primula*), do not thrive particularly well in gardens, and certain species die after a short time even when cultivated with the greatest care. Yet the hybrids of such species flourish wonderfully well under similar circumstances. They blossom luxuriantly, and may be kept in a state of vigorous growth for many years. Examples of this are afforded by *Primula pubescens* and *Primula Venzoi*. One of the parent-stocks of *P. pubescens*, viz. *Primula hirsuta*, can only be reared if the soil used is expressly prepared for itself, and if several other special precautions are taken, whereas the hybrid, *P. pubescens*, grows exuberantly in ordinary garden-soil. The case of *P. Venzoi*, the hybrid-offspring of *Primula tyrolensis* and *Primula Wulfeniana*, is still more remarkable. Although both the parent species are reared with difficulty, even when the greatest care is bestowed upon their cultivation, *Primula Venzoi* will flourish with extreme luxuriance if planted close to them in the same soil and under the same external conditions.

Another phenomenon sometimes exhibited by hybrids is a change in the distribution of the sexes. It often happens, for instance, that hybrids produce pseudo-hermaphrodite female flowers and pseudo-hermaphrodite male flowers (*cf.* p. 294), even where both parent-species have true hermaphrodite flowers. In Willow hybrids a partial transformation of male into female flowers, and *vice versâ*, has been not infrequently observed, and we then have monœcious catkins bearing flowers, half of which are female and half male. This change also occurs in true species, but only as a rare exception, whilst in the case of hybrids it is by no means uncommon.

Hybrids also exhibit the phenomenon known as the "doubling" of flowers, which depends upon the transformation of stamens into petals, independently of the action of tiny gall-mites, which are the frequent cause of doubling in other plants (*cf.* p. 548). Several hybrid Roses, Pinks, and Camellias are only known with double flowers.

It is difficult to explain the fact, repeatedly confirmed by observation, of the appearance in hybrids of characters which are not present in either parent-species, or rather which cannot be traced to inheritance from either of those species. Thus it sometimes happens that individual plants of a hybrid develop sinuate foliage-leaves with wavy outline, though in both of the parent-species the leaves are either entire or only slightly toothed. The hybrid *Salvia sylvestris* occasionally exhibits deeply sinuate radical leaves, whilst *Salvia nemorosa* and *Salvia pratensis*, the two species to which it owes its origin, never do so. Another instance of the same kind is that of a Stock, the hybrid of *Matthiola incana* and *Matthiola Maderensis*. Neither the one nor the other parent-species has sinuate leaves, yet here and there plants of the hybrid display foliage with the margins so deeply cut as to remind one at first sight of *Matthiola sinuata*. Again, in *Primula pubescens* the leaves are sometimes more deeply sinuate than in either *Primula Auricula* or *Primula hirsuta*. In hybrids of the Foxglove genus (*Digitalis*), flowers not infrequently make their appearance wherein the corolla is produced underneath into a spur as in the Toad-flax (*Linaria*). One hybrid produced by crossing two species of Water Lily, *Nymphæa Lotus* and *Nymphæa dentata*, displayed dark violet lines on its sepals which are not to be seen in either parent-species. Reference must also be made to the comparative frequency with which hybrids bearing white flowers spring from species with blue, violet, red, or yellow blossoms whose non-hybrid offspring only produce colourless flowers on very rare occasions. Lastly, we may mention the fact that as from species so also from hybrids varieties may be formed; but they have no permanence amongst the descendants of a race, passing into other varieties whenever it undergoes the restrictive influence of a change in external conditions.

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3. THE ORIGIN OF SPECIES.

Genesis of New Species.—Derivation of Existing Species.—The Sub-divisions of the Vegetable Kingdom.

THE GENESIS OF NEW SPECIES.

It is now more than forty years since I discovered, on an island on the Danube not far from the little town of Dürenstein, a Willow which had till then remained unknown to Botanists. The plant in question was growing on the island in company with a number of other Willow-trees and Willow-shrubs belonging to the

species known as *Salix incana* and *Salix daphnoides* respectively, and it was apparently intermediate in form between those two species. The hairs, the system of ramification, the foliage, and the flowers resembled those of *S. incana* in some respects and those of *S. daphnoides* in others, and a single glance would have led any unbiassed observer to conjecture that he had to deal with the product of a cross between these two species.

This discovery,[1] made in one of the first years of my career as a student of Botany, chanced upon a time when Botanists were beginning to take a particularly keen interest in all cases of intermediate forms observed growing in a state of nature. Some of the leading men at that time refused to believe in the existence of any wild hybrids, and were of opinion that the supposed cases were *varieties* of species whose presence was to be explained by a tendency in the plant itself to change its form. They also held the view that all plants between which one or more intermediate forms had been found to exist were to be included in a single species, and, in accordance with this, they not infrequently treated three, four, or more kinds of plant previously classed as distinct species as being really "varieties" of a single species, because forms obviously intermediate between them, *i.e.* so-called "transitional forms", had been discovered. This practice was carried so far that several systematic Botanists of that day included in one species 5, 10, and even 15 distinct Hawkweeds which had been previously described as separate species, the reason for the change being that they were all linked together by transitional forms. Another school of Botanists, on the other hand, recognized in most of the so-called transitional forms the results of natural crossing, but they did not deny the existence in plants of a capacity to form varieties in the Linnean sense in response to changes of soil or climate.

To my mind even at that time there could be no doubt which of the two opposing theories concerning the genesis, significance, and position of intermediate forms was to be preferred. The discovery of the hybrid Willow referred to led to my paying particular attention to plant-hybrids, and in the course of the last forty years I have made extensive series of experiments to clear up many obscure points, and to correct the prejudices which then prevailed.

One misconception as to the nature and significance of hybrids, which had great weight and found expression in the name of "bastard" assigned to them, consisted in the idea that they were contrary to nature. The German word "bastart" is defined by Grimm as a base and useless species. This prejudice was carried so far that Kant positively denied their independent existence, and believed they must necessarily die out with the first generation. Connected with this notion was another, according to which hybrids were destitute of the power of producing fertile seeds and propagating their kind sexually. It probably arose from observation of the hybrids of the Mullein genus (*Verbascum*), which in Central Europe are so common

[1] The little paper recording the finding of this Willow, with some additional remarks, by Anton Kerner, was published in 1852 (Vienna, Zool. Bot. Ver. Verhandl. II., 1852). This seems to have been Kerner's second definite contribution to science; what would appear to be his first is printed in the same publication a few months previously.

and conspicuous that they were accepted as the results of crosses between two species even by those amongst the earlier Botanists who were most disinclined to recognize the existence of plant-hybrids. Now, these Mullein hybrids do not for the most part mature any seeds. The pistil itself is usually incompletely developed, and even if one or other of the fruit-capsules does develop, the ovules in it are abortive and infertile. Nevertheless it would be erroneous to say that no Mullein hybrid has ever produced seeds capable of germination. Two such hybrids were artificially generated in my garden, viz.:—*Verbascum rubiginosum*, by crossing *Verbascum Austriacum* with the pollen of *Verbascum phœniceum*, and *Verbascum pseudophœniceum*, by crossing *Verbascum Blattaria* with *V. phœniceum*. The former of these hybrids, it is true, never produced seeds capable of germination; but in the case of the second, although most of the capsules were empty and abortive, a few containing fertile seeds ripened; so that even the hybrids of Mulleins are not invariably sterile.

Anyone who will look beyond the limited range of that particular genus will be convinced that in respect of their capacity for sexual reproduction hybrids do not differ essentially from plants which have been admitted to be "true", permanent species by Botanists of all periods. For the case of a few of these true species, as, for instance, *Cochlearia Armoracia*, *Crambe tataria*, *Lilium bulbiferum*, *Lysimachia Nummularia*, *Rubus odorus* and *R. Nutkaensis*, it has long been known that if the stigmas are dusted with pollen from the stamens in the same flowers very few seeds, if any, are set, whilst pollen from other flowers is obviously preferred by them. On the other hand, there are true species whose flowers are pseudo-hermaphrodite, i.e. they have the appearance of being bisexual, but are really unisexual (*cf.* p. 294). In one individual we find that the ovaries are fully developed, as also the stamens, but that no pollen capable of fertilizing ovules is produced in the anthers; in another plant the ovaries are imperfectly developed, whilst the anthers are filled with effective pollen. For seeds to be set in such circumstances two individuals at least are requisite, and pollen from a plant bearing pseudo-hermaphrodite male flowers must be transferred to the stigmas of the pseudo-hermaphrodite female flowers. Now *hybrids* with pseudo-hermaphrodite flowers also exist, and in their case, as in that of true species, two kinds of individual are requisite to produce seeds capable of germination. Supposing, however, in such a case that the two kinds of plant necessary for reproduction do not grow close together or do not flower simultaneously, or that one of them is altogether absent—a contingency which must often occur—fertilization cannot be effected, and consequently no seeds can be formed. It is scarcely necessary to amplify the proposition that dicecious hybrids behave in this respect in the same manner as true species, and that pollination and fruit-formation may in them be impeded likewise by dichogamy or by heterostylism. In many hybrids, again, as in true species, the relative positions of stamens and pistil, the height of the stigma, the length of the filaments, and other conditions of the kind are not conducive to autogamy, and consequently no transference of pollen from the anthers to the stigmas in the same flower can take place

either at the beginning or at the end of the period of bloom. Such hybrids are dependent upon foreign pollen, and if none is brought at the right time by wind or insects no pollination or fertilization takes place, and no seeds are developed.

Even these brief references to recently-discovered phenomena connected with fertilization are sufficient to indicate that the suppression of the function of fruit-formation in hybrids is due in most cases to the same causes as operate on true species. Innumerable experiments have proved that if at the proper time pollen of the right sort is placed upon the stigmas of hybrids fertile seeds are developed as in the case of true species.

We must now consider a statement which for long held its place in Botanical works owing to the positive manner in which it was enunciated by an eminent authority. The proposition in question, whilst admitting the fertility of hybrids, asserted that it was conditional on the stigmas being supplied with pollen from one or other of the parent-stocks, and that no fruit was formed as a result of autogamy. This assumption rested partly on certain series of experiments performed on garden-plants by the Botanist Koelreuter in the second half of the eighteenth century.[1] By crossing two species of Tobacco-plant (*Nicotiana rustica* and *Nicotiana paniculata*) Koelreuter produced a hybrid which in its characteristics was an exact mean between the two parent-species. The stigmas in the flowers of this hybrid were then dusted with pollen from one of the parents, and the result of this second cross was another hybrid, the characters of which resembled those of the species which supplied the pollen more closely than was the case with the first hybrid. The same treatment was applied to the second hybrid, and thus, after three generations, a plant was evolved completely resembling the male progenitor. The first hybrid had, therefore, in a sense, "reverted" to that particular parent-species. The "reversion" of the hybrid to the other parent-species was similarly procured after three generations. Such a result could naturally not have ensued if the action of the pollen of the parental stocks on the hybrid had not been entirely effectual. It is accordingly quite true that hybrids are fertile when the pollen used to fertilize them is taken from either of the parent-species, but the further assertion that they are sterile if their own pollen is employed for the purpose is incorrect, at any rate as a universal proposition. Koelreuter's own conscientious experiments show conclusively that it is possible for hybrids to bring fruits to maturity as a result of autogamy, and that, as a matter of fact, the majority do develop such fruits. We may also refer to the large number of plants with ornamental flowers, such as Begonias, Pansies, and Pinks, which every year in our gardens produce seeds autogamously, and are reproduced in great numbers by means of those seeds (see p. 556). Some interesting experiments have also been made on *Medicago media*, the hybrid of *Medicago falcata* and *M. sativa*. This plant, which is, in many places, cultivated on a large scale for fodder, is propagated continuously by seeds which are in a very

[1] Joseph Gottlieb Koelreuter (1733–1806) was the first to investigate the question of hybridization scientifically and thoroughly. His work, which ranks with the best of modern times, is contained in his *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen* (published 1761–1766); a convenient reprint was issued in 1893.

subordinate degree, if at all, dependent on the parent-species for their production. Nay more, it would be prejudicial were one of those species to supply the pollen seeing that the fertility of this hybrid is diminished thereby. We have here a case of a hybrid manifesting enhanced fertility as compared with one of its parents; for *Medicago falcata* is one of those Papilionaceæ in which autogamy is attended with very small result. It has been ascertained that in cases where the flowers of that species are thrown upon their own resources for pollen, out of every 30 flowers only two or three fruits containing seeds capable of germination are matured. If flowers of *Medicago falcata* are crossed with pollen belonging to another species, such as *Medicago sativa*, a much larger number of fruits is produced, and it is stated that the number of seeds is almost doubled. *Medicago media* usually sets from six to eight pods in each raceme if the flowers depend upon their own pollen for fertilization. If, however, pollen is brought to them from *Medicago falcata* the degree of fertility is strikingly reduced; the flowers so crossed either remain quite empty or develop pods whose seeds are not capable of germination. *Medicago media* is therefore an instance of a hybrid which is actually injured by being crossed with one of the parent-species, but is successfully reproduced by autogamy. The upshot of all these experiments is that the results of autogamy are no different in hybrids from what they are in species.

We may infer from the same experiments in what way reversions of hybrids to their parent-species should be regarded. Botanists possessed with the idea that every hybrid was the product of some process contravening the laws of nature imagined that this anomaly must be counteracted, and that this was effected by a tendency existing in the hybrid's descendants to approximate sometimes to one and sometimes to the other parent-species, so that in the course of a few generations they would completely revert to the form of a true species. As the accounts given by gardeners seemed to confirm the fact of the occurrence of such reversions, no doubt was raised as to the soundness of this view. The reports of gardeners on the subject were, however, founded on inaccurate observation, want of knowledge, and self-deception. In former years the phenomena of pollen-transport in the case of pseudo-hermaphrodite, dichogamous, and heterostyled flowers, and many other things connected therewith, were not appreciated at their full value; to most gardeners they were altogether unknown, and it was only in the rarest instances that any measures were taken to preserve the species and hybrids reared in gardens from extraneous pollen. The majority of growers had no suspicion that the fruit formed on a particular cultivated hybrid might be due to the effect of pollen conveyed by the wind or by insects from one of the parent-species flourishing in the vicinity, and if they noticed that the seedlings arising from that fruit exhibited characteristics approximating to either of the parent-species they were in the habit of calling the phenomenon a reversion. But if a gardener takes care that the flowers of a hybrid under cultivation are only supplied with pollen developed in flowers of their own kind whilst that of other species is excluded, the plants which arise from the seeds of the hybrid exhibit the characters of that hybrid unaltered. Thus,

hybrids prove true to seed, to use a gardener's expression, and there is no truth in the assertion that they have an innate tendency to revert to one of the parent-forms.

At one time the attempt was made to distinguish two sorts of hybrids—those arising between *species*, which were regarded as sterile, and those arising between *races*, which were regarded as fertile. By "races" are understood forms which, whilst not differentiated by characters of sufficient importance to rank as species, are yet reproduced by seed and transmit their characters to their offspring. They seem to stand midway between what are called varieties and sub-species. Forms arising by the crossing of species were termed hybrids, those arising by the crossing of races "blendlings". But in this matter Botanists argued in a hopeless circle. Firstly, it was said that if races were crossed the intermediate forms were fertile; whilst those springing from species were sterile; and, secondly, the distinction between races and species was defined as consisting in the fact of the fertility of the intermediate forms produced by crossing races, as compared with the infertility of those derived from crosses between species. A distinction founded on such reasoning as this is, of course, destitute of any value or meaning. What, then, is the difference between races and species? There are certain forms which have a similar physiognomy, an agreement in certain striking particulars. They are bound together by these common characteristics into a single group, and it must be supposed that they are nearly allied in respect of their origin also. But no more than *affinity* can be predicated by characters which, though perhaps less striking than the others, are yet transmitted unmodified to descendants and prove themselves to be constant attributes. It has been sought to apply the term "races" to nearly akin forms of the kind. But the degree of variation has nothing to do with the conception of a species; the essential point is that the characters wherein the variation is manifested are transmitted unchanged to the descendants, and this happens as a fact in all the cases to which the name of race has been affixed. The use of the term would obviously imply quite a different connotation of the name of species from that which Linnæus, with logical exactitude, attached to it. According to him a species was not an assemblage of individuals of the same form, but an assemblage of individuals of different forms, constituting a group of units and not itself the unit of the system. If, like the French system, we were to distinguish the groups of nearly allied species as "petites espèces" from those exhibiting more marked differences and less nearly akin to one another, which would be known as "grandes espèces", that would involve quite sufficient recognition of the difference which exists in various degrees between members of the two categories in question; but the introduction of the word "race" side by side with the word "species" suggests the idea of some line of demarcation between the two such as does not in reality exist. Again, if there is no definite boundary between race and species the separation of blendlings from hybrids also fails, and with it the proposition that only those hybrids are fertile which are the offspring of races.

In respect of fertility, then, there is no difference between hybrids and species.

In the one as in the other we find those floral contrivances for bringing about cross-fertilization in the first place and autogamy in the second, of which an account was given in the first part of this volume; in the one case as in the other cross-fertilization often takes place as a result of those contrivances, and both categories include forms which are incapable of self-fertilization, and only develop fruits and fertile seeds in consequence of geitonogamy or xenogamy. Seeing that it has been ascertained also that, provided the pollen from other species is excluded, hybrids transmit their form unchanged to their posterity, and that the substitution of brood-bodies for fruits as a means of reproduction and the enhancement of the development of those bodies in the event of there being no fruit, are phenomena common to species also, we come to the conclusion that no line of demarcation between hybrids and species exists in respect of the function of propagation.

The consideration of all these facts led me years ago to raise the question whether hybrids could originate species,[1] and to answer it in the affirmative. Looked at from this point of view, the hybrids which have been and are being produced in nature acquire a special significance, and it becomes important to form a correct notion as to their existence, behaviour, and distribution in localities where the life of plants is untrammelled and undisturbed. Only the vegetation of Europe has been thoroughly studied in this connection, yet this alone affords a fund of information, and we may take it for granted that what is true for Europe will apply likewise to the other quarters of the globe.

We shall be rather below than above the mark if we estimate at a thousand the number of wild hybrids belonging to the Flora of Europe which have been brought to light during the last forty years. Of these only a small proportion are of the class of Cryptogams, but this circumstance is due to the fact that it is only lately that Botanists have paid any attention to hybrid Cryptogams. Future researches will no doubt establish the hybrid nature of many so-called "transitional forms". Amongst Mosses in particular, several hybrids arising from species which grow in ditches and marshy places (*Hypnum aduncum*, *H. fluitans*, *H. lycopodioides*, &c.) have been discovered. A few hybrids of the genera *Orthotrichum*, *Grimmia*, *Physcomitrium*, and *Funaria* have also been identified. Fern hybrids are known in the genera *Aspidium*, *Asplenium*, *Ceterach*, *Polypodium*, and *Scolopendrium*. *Scolopendrium hybridum*, which was observed in Istria, is especially remarkable as being the result of a cross between two species possessing widely different forms and included in different genera. The parent-species of this hybrid are, firstly, *Scolopendrium officinarum*, which is glabrous and grows in clefts in damp, shady rocks and walls; and, secondly, *Ceterach officinarum*, which has the under surfaces of its fronds thickly covered with brown scales and flourishes in the crevices of dry walls exposed to the sun. Amongst the Horse-tails we may mention *Equisetum inundatum*, a rather common hybrid, which owes its existence to the crossing of *Equisetum arvense* and *E. limosum*.

In the division of the Coniferæ no less than seven hybrids have been recently

[1] Oesterreich. botanische Zeitschrift xxi. p. 34 (1871).

identified, and this fact is of no little significance when taken in connection with the circumstance that Europe only possesses 41 species of Conifers. *Juniperus Kanitzii*, the hybrid offspring of *Juniperus communis* and *J. sabinoides*, is a very instructive instance owing to the great diversity in the form of the two parent-species.

Comparatively few hybrids occur amongst Grasses. The majority belong to the genus *Calamagrostis*. Strangely enough, most hybrid grasses have arisen from crosses between species of different genera, as, for instance, *Festuca* and *Lolium*, *Triticum* and *Elymus*, *Triticum* and *Ægilops*. The hybrid derived from *Ægilops ovata* and *Triticum sativum*, and known by the name of *Ægilops triticoides*, and the hybrid *Ægilops speltæformis*, obtained by crossing *Ægilops triticoides* with *Triticum sativum*, have been the subject of lively discussion in their time, and have contributed not a little to clearing up our ideas concerning hybrids. As a set-off to the Grasses, the groups comprising Reeds, Rushes, and Sedges include a comparatively large number of hybrids. For example, in the genus *Carex* instances have been discovered in the most widely different localities.

Amongst Liliflorеæ and Irideæ only a few wild hybrids have been found, but on the other hand a large number occur amongst Orchidaceæ all over Europe. It is striking how many of these Orchid hybrids spring from species which are placed by Botanists in different genera. Hybrids are known, for instance, which are derived respectively from *Aceras* and *Orchis*, from *Anacamptis* and *Orchis*, from *Cœloglossum* and *Orchis*, from *Gymnadenia* and *Orchis*, from *Himantoglossum* and *Orchis*, from *Serapias* and *Orchis*, from *Gymnadenia* and *Nigritella*, and from *Epipactis* and *Cephalanthera*. The hybrid *Epipactis speciosa*, lately discovered in the Erlafthal of Lower Austria, is the result of a cross between *Epipactis rubiginosa* and *Cephalanthera alba*, and is of special interest on account of its manifesting characters strongly resembling those of species indigenous to regions at a great distance from the place where the hybrid occurs, for at first sight *Epipactis speciosa* might easily be taken for *Epipactis gigantea*, which is a native of North America, or for the Japanese species named *Epipactis Thunbergii*.

Hybrids are comparatively numerous amongst the Pond-weed group (*Potamogeton*). These are aquatic plants which discharge their pollen in the form of clouds of dust, and at the season of pollination raise their flowers above the surface of the water. Owing to their being completely protogynous (see p. 310), autogamy is out of the question. The crossing of pairs of species is especially promoted by the circumstance that the different species flower in definite succession, so that always just at the time that one species is terminating its period of bloom another is coming into flower.

Plants which have their flowers in catkins (*amentaceous*), such as Oaks, Birches, Alders, Poplars, and Willows, produce an uncommonly large number of hybrids. In Willows pollination is effected by insects, in the other genera by the wind. This gives occasion for us to raise, in connection with this group, the question whether hybrids originate more frequently from entomophilous or from anemophilous plants.

The fact that many more than a hundred Willow hybrids are known looks as if the agency of insects were the more favourable to hybridization. At the same time we must bear in mind that the number of species of Willow in Northern and Central Europe is very large, whilst the number of different Birches, Alders, and Oaks is small. Taken in relation to the number of species, the hybrids belonging to the plants last mentioned are no less numerous than those of Willows, and it appears, therefore, that hybrids occur as frequently amongst plants whose pollen is dispersed in the form of dust as amongst plants with adhesive pollen which is transported by insects. The prevalence of hybrids amongst Pond-weeds points to the same conclusion. A comparison between the Docks and Polygonums even indicates that in anemophilous plants, such as the Docks, hybrids come into existence more readily than in the case of entomophilous plants as represented by the Polygonums, for in scarcely any genus is the number of hybrids so great in proportion to the number of species as in the Dock genus, and the ratio is certainly higher than it is with the Polygonums.

As regards the Caryophyllaceæ it is remarkable that *Dianthus* has many hybrids and *Silene* few, although these two genera resemble one another in the distribution of their sexes and in being chiefly visited by lepidopterous insects. In the genus *Viola* hybrids are extremely common. It has been shown that many Violas which were formerly designated as "transitional forms" are in reality hybrids, and thus the grounds upon which systematic Botanists treated whole series of species as one only are removed. As with the Violas in Central Europe so also with their allies the Cistuses in the South, hybrids are numerous; several kinds of *Cistus* hybrids occur so commonly that they were described as species by the Botanists of former times.

It is noticeable in the Cruciferæ that no hybrids are formed in nature between the numerous annual species of this family. There are also only a few hybrids known which are derived from the perennial species. The genera *Roripa* and *Draba* are, however, exceptional in this respect. The case of Ranunculaceæ is similar. In the comprehensive genera *Aconitum*, *Helleborus*, and *Ranunculus*, only a few hybrids have been identified with certainty, whilst in *Anemone* and *Pulsatilla* there are almost as many hybrids as species. The case of the hybrid Water-lily *Nuphar intermedium* will be discussed later on.

Many hybrids are known in the genera *Tilia*, *Hypericum*, *Malva*, *Rhamnus*, *Pistacia*, *Acer*, *Euphorbia*, and *Epilobium*, the last alone including fifty different kinds. This makes it all the more remarkable that so varied a family as the Umbelliferæ yields very few hybrids. Of the numerous hybrids belonging to the Saxifragaceæ we may mention as specially noteworthy those derived from species which differ exceedingly from one another in form and size. One cannot easily imagine two plants in the limits of a single genus which present a greater contrast to one another in respect of flowers, leaves, and general mode of growth than is exhibited in the following cases:—*Saxifraga cæsia* and *S. mutata*, *S. Aizoon* and *S. cuneifolia*, *S. aizoides* and *S. squarrosa*, and yet hybrids have sprung from the crossing of these species.

About two hundred hybrids, for the most part fertile, have come into existence in nature within the family of the Rosaceæ. The genera *Geum*, *Potentilla*, *Rubus*, *Rosa*, and *Sorbus* are inexhaustible in the formation of hybrids. On the other hand, the Papilionaceæ, a family allied to the Rosaceæ, is peculiarly wanting in hybrids.

This discrepancy between nearly-related families in respect of the number of their hybrids is again noticeable in the class of plants known as the Monopetalæ. The Labiatæ, *e.g.* the genera *Ajuga*, *Prunella*, *Calamintha*, *Lamium*, *Marrubium*, *Mentha*, *Salvia*, and *Stachys* include numbers of hybrids, whilst the Boraginaceæ have very few. Of the latter only one or two hybrids are known, and these belong to the genera *Pulmonaria* and *Symphytum*. The Scrophulariaceæ and Rhinanthaceæ have long been noted for the great variety of their hybrids; the genera *Pedicularis* and *Verbascum* in particular exhibit a great wealth of forms, *Pedicularis* in alpine regions and *Verbascum* on the shores of the Mediterranean. *Verbascum* alone includes more than fifty. In the case of Gentianaceæ, also, the products of a great number of different crosses are found in the Alps, the chief parent-species being the long-stalked *Gentiana lutea*, *G. Pannonica*, *G. punctata*, and *G. purpurea*. Primulaceæ, whether growing on the upper or the lower levels of mountains, are famous for the abundance of their hybrids. In the genera *Androsace*, *Primula*, and *Soldanella* the number of hybrids identified by Botanists surpasses the number of the species from which they have sprung. The Ericaceæ, although comparatively poorly represented in Europe, exhibit several hybrids derived from the genera *Erica*, *Rhododendron*, and *Vaccinium*.

Hybrids are also specially numerous in the family of the Rubiaceæ, the genus *Galium* being the most prolific in this respect. But the greatest number of all is to be found amongst the Compositæ. More than two hundred hybrids have been identified in the genera *Achillea*, *Carduus*, *Centaurea*, *Cirsium*, *Hieracium*, *Inula*, and *Lappa* alone. Of hybrid Compositæ the following are particularly worthy of notice: — *Erigeron Hülsenii*, which is the result of a cross between *Erigeron Canadense*, an annual species brought into Europe from America, and *Erigeron acer*, a perennial species indigenous to Europe, and, secondly, the Cudweed hybrids, *Filago mixta*, *F. neglecta*, *F. subspicata*, &c., which spring from crosses between annual species, and are, therefore, exceptional, for annual species in general rarely produce hybrids.

In many cases only a few individual instances of these natural hybrids have been observed; in some, indeed, one single specimen alone has as yet been discovered. The majority, however, grow by the hundred or by the thousand in the localities proper to them, and many are represented by immense numbers of plants, and possess a wide area of distribution. *Salvia betonicifolia*, a hybrid derived from *Salvia nemorosa* and *S. nutans*, occurs as commonly as its progenitors in places on the grassland in the central parts of Siebenbürgen (Hungary); *Marrubium remotum*, a hybrid of *Marrubium peregrinum* and *M. vulgare*, is to be found everywhere on the plains of South-Eastern Europe, especially in the flat country by the Theiss and

the lower Danube; *Roripa anceps*, the hybrid of *Roripa amphibia* and *R. sylvestris*, is met with all over the district forming the basin of the Baltic; *Primula digenea*, a hybrid derived from *Primula vulgaris* and *P. elatior*, grows in its thousands in the upland meadows of the Eastern Alps; *Betula alpestris*, produced by the crossing of *Betula alba* and *B. nana*, is met with in great abundance in the Jura, in Scandinavia, and in the North of Russia, and here and there entire copses are composed of it; *Nigritella suaveolens*, a hybrid produced from *Gymnadenia conopsea* and *Nigritella nigra*, is so common in the Central Alps, for instance, in the Pusterthal of Tyrol, that hundreds of specimens are sometimes encountered in a single meadow; *Primula Salisburgensis*, the hybrid of *Primula glutinosa* and *P. minima*, is represented by a host of plants on the Tyrolese Alps, as, for instance, on the Muttenjoch and the neighbouring mountains which separate the Gschnitzthal from the Obernbergthal.

Several hundreds of other cases of the kind might be mentioned, but the limits of this book will not allow me to do more than give the following names selected from the long list that lies before me:

HYBRID.	PARENTS.
Asplenium Germanicum	*Asplenium Ruta-muraria* × *A. septentrionale.*
Calamogrostis acutiflora	*C. arundinacea* × *C. epigeios.*
Carex Bœnninghausiana	*C. paniculata* × *C. remota.*
Scirpus Duvalii	*S. lacustris* × *S. Pollichii.*
Juncus diffusus	*J. effusus* × *J. glaucus.*
Orchis Dietrichiana	*O. tridentata* × *O. ustulata.*
Potamogeton spathulatus	*P. polygonifolius* × *P. rufescens.*
Populus canescens	*P. alba* × *P. tremula.*
Salix Austriaca	*S. grandifolia* × *S. purpurea.*
Rumex maximus	*R. aquaticus* × *R. Hydrolapathum*
Polygonum mite	*P. Hydropiper* × *P. Persicaria.*
Cistus Florentinus	*C. monspeliensis* × *C. salvifolius.*
Draba Hoppeana	*D. Fladnizensis* × *D. Carinthiaca.*
Roripa stenocarpa	*R. palustris* × *R. sylvestris.*
Pulsatilla Hakelii	*P. patens* × *P. pratensis.*
Drosera obovata	*D. longifolia* × *D. rotundifolia.*
Epilobium salicifolium	*E. alsinifolium* × *E. montanum.*
Sorbus latifolia	*S. Aria* × *S. torminalis.*
Potentilla procumbens	*P. erecta* × *P. reptans.*
Mentha nemorosa	*M. aquatica* × *M. sylvestris.*
Pedicularis atrorubens	*P. incarnata* × *P. recutita.*
Verbascum rubiginosum	*V. Austriacum* × *V. phœnicum.*
Acanthus spinulosus	*A. mollis* × *A. spinosissimus.*
Gentiana Charpentieri	*G. lutea* × *G. punctata.*
Primula pubescens	*P. Auricula* × *P. hirsuta.*
Vaccinium intermedium	*V. Myrtillus* × *V. Vitis-idaea.*
Erica Mackayi	*E. ciliaris* × *E. Tetralix.*
Cirsium tataricum	*C. canum* × *C. oleraceum.*
Lappa pubens	*L. minor* × *L. tomentosa.*
Hieracium stoloniflorum	*H. aurantiacum* × *H. pilosellæforme.*

The fact that hybrids exhibit every conceivable degree of frequency of occurrence might lead one to suppose that the rare hybrids were those that had been most recently produced, and that they exist only as isolated plants because they have not

yet had time to disperse and multiply. This conception would not, however, accord with the actual condition of affairs. In point of fact, the floral contrivances which exist for promoting crosses between different species occasion a constant origination of hybrids, but it is certainly not the case that they all have the prospect of becoming new species. Many are called, but few are chosen. In only a fraction of the total number of fresh plant-forms produced yearly by inter-specific crosses do we find the power to survive and multiply. The first condition that must be fulfilled if a hybrid is to become a species is that it be fertile, *i.e.* that its flowers yield seeds capable of germination as a consequence of fertilization with their own pollen. By "their own pollen" is here meant not only that which is developed in the same flower as the stigma which receives it, or in some flower on the same plant, but also pollen belonging to other plants provided they belong to the same hybrid-formation. To this condition another is added in the case of dicecious, pseudo-hermaphrodite, and completely dichogamous flowers, viz.: that several individuals of the hybrid must make their appearance at the same time, and that of these at least one must bear male flowers and one female flowers. If we suppose the case of a Willow hybrid, of which all the individual-plants bear catkins of male flowers only, obviously no propagation by means of fruits is possible. If none but female flowers are borne, these may be crossed with the parent-species and give rise to goneoclinic hybrids (cf. p. 559), and perhaps, in addition, ternary hybrids may be produced, but no unmodified descendants can be expected from the fruits of a Willow of the kind. The same thing applies in the case of *Cirsium*, the separate individuals of this genus being differentiated into those bearing pseudo-hermaphrodite male flowers and those bearing pseudo-hermaphrodite female flowers (see p. 294). This affords sufficient explanation of the fact that although Willows and Cirsiums are continually developing numberless hybrids, few instances are known which one can affirm to be the beginnings of new species. It usually happens, in fact, in the case of these hybrids, that all the plants which arise together at a particular spot are furnished exclusively either with true or pseudo-hermaphrodite male flowers, or else with true or pseudo-hermaphrodite female flowers. The goneoclinic hybrids produced from the latter are for the most part represented by greater numbers of individuals. Moreover, amongst those individuals both sexes much more frequently make their appearance; hence, they have a far better prospect of being preserved.

The development of a hybrid into a species is also dependent on the conditions determined by the habitat. When a species thrives well at a particular place, is represented by a large number of individual plants, and renews itself in descendants which are in the main unchanged, it may be assumed that the organization of that species is suited to the soil and climate of the habitat in question. If there were no such harmonious relation there could be no question of the species flourishing, but on the contrary is would sooner or later die out. This suitability of the climate and soil to the organization manifested in the plant's external form must also exist in the case of the newly developed hybrid if the few individuals which spring up at any particular place are to survive in their original settlements, and to give rise to

a numerous progeny. Sometimes such suitability does exist, but sometimes also it does not. In the latter case the hybrid is suppressed as soon as it sees the light. But even if its organization is adapted to the soil and climate of the place of origin, it has to enter upon a struggle with the species already established there, and especially with its own parent-species. If the latter grow luxuriantly and in large numbers at the spot, it is not easy for the new form to take possession of the ground. In two cases only is there any prospect of the place of origin becoming a permanent home for the hybrid's descendants: firstly, where the hybrid, in virtue of its particular attributes, is equally well, or perhaps even better adapted to the habitat of the parent-species than are the plants already established there, and secondly, when the hybrid originates at a spot more or less removed from the place where the parent-species grow and encounters conditions of soil and climate which agree with it better than with the parent-species.

That these conditions of the origin of species from hybrids are sometimes fulfilled will now be shown by a few examples. In the Tyrolese Alps, to the south of Innsbruck, at the head of the valleys known as the Stubaithal and the Gschnitzthal, there are certain mountains which rise steeply to a height of from 2500 to 3000 metres. The base of these mountains is composed of crystalline schist; midway up their ascent mixed strata of schist and limestone are encountered; and above these strata there is limestone and also dolomite, rising abruptly and forming the peaks and ridges. Half-way up the sides, where the soil exhibits great variety, an extraordinarily rich flora is developed. Plants which are, except in this instance, peculiar to schist formations, and others usually only found on limestone, here grow close together. Amongst other species the Alpine Roses, *Rhododendron ferrugineum* and *R. hirsutum*, grow side by side on the same soil and on the same slopes. Associated with them is a third species of Alpine Rose, *Rhododendron intermedium*, which has sprung from the crossing of *R. ferrugineum* and *R. hirsutum*. At several places, *e.g.* on the eastern and northern slopes of the Hohe Burgstall, in the Stubaithal, and on the Padaster Alp in the Gschnitzthal, *Rhododendron intermedium* occurs more commonly than either of the parent-species. Like the latter, it grows on soil rich in humus, flowers abundantly, develops fruits with fertile seeds, and transmits its characteristics unaltered to its descendants. Here and there isolated plants are found which must be ranked as goneoclinic hybrids, but plants of *Rhododendron intermedium* form the larger proportion of the Alpine Roses which clothe the mountain-sides. This form accords in every particular with the requirements demanded of a species, and is quite as much a systematic entity as either *R. ferrugineum* or *R. hirsutum*. The following is the explanation of how this has come to pass: The colour of the flowers is a little lighter than in *R. ferrugineum* and richer than in *R. hirsutum*; it is a brilliant carmine tint, and enables one even at a distance to identify every plant of the hybrid. Hive- and bumble-bees hovering about in search of honey are more attracted by flowers of *R. intermedium* than by the others, owing to the superior brilliancy of their coloration, and the result is that these flowers are

crossed with pollen of their own kind. If no insects appear upon the scene, autogamy takes place. In either case fertile seeds are developed, and give rise to plants which do not differ from the parent-form. In places where detritus from the adjacent limestone and dolomitic cliffs is mixed with the humus of the soil the seedlings thrive distinctly better than those of *R. ferrugineum* and no less well than those of *R. hirsutum*. Thus, so far as the soil is concerned, *R. intermedium* has an advantage over *R. ferrugineum*, and in respect of insect-visits it is better off than either of the parent-species. These advantages, though apparently insignificant, are not merely sufficient to prevent *R. intermedium* from yielding to the parent-species in the struggle for existence at the places in question, but even give it rather a better chance of prevailing.

As a second instance, we will take *Salvia sylvestris*, the hybrid offspring of *Salvia nemorosa* and *Salvia pratensis*. This plant grows in dry meadows all over the low country to the south of Vienna, as, for instance, on the banks of the river Leitha, which separates Austria proper from Hungary. The landscape there is slightly undulating, the elevations are composed of boulders and clay, and wherever the latter is present in great quantities, especially on the gentle slopes of the rising ground, *Salvia nemorosa* constitutes an important item in the vegetation. The hollows are full of a dark moist earth, with a rich admixture of humus, and there we find meadows in which *Salvia pratensis* grows luxuriantly. These two kinds of habitat usually pass quite gradually into one another, and the parts common to both consist of dry meadow-lands. *Salvia nemorosa* does not thrive in the intricate grass-carpet of these meadows, and is rarely to be seen there, whilst for *Salvia pratensis* the soil is too dry, so that that species also is but poorly represented on the areas in question. On the other hand, these dry meadows are the most suitable ground for the hybrid *Salvia sylvestris*, and it thrives exceedingly upon them. Its flowers are much visited by insects; its fruits ripen in as large numbers as in the case of *S. nemorosa* or *S. pratensis*, and have been found by experiment to be fertile in a proportion of more than 60 per cent. *Salvia sylvestris* has therefore scattered itself all over this dry meadow-land, and manifests all the characteristics essential to our conception of a species.

A third example is *Nuphar intermedium*, a hybrid derived from *Nuphar luteum* and *Nuphar pumilum*. This plant grows in lakes in the Black Forest and in the Vosges. It is also scattered over North Germany, and occurs with increasing frequency in Central and Northern Russia and in Sweden. It has been found as far north as Lapland. At the northern extremity of this large area of distribution *Nuphar intermedium* is more abundant than the species from which it is derived; indeed in many places it occurs in their absence, and in fact passes beyond the northern limits of their area of distribution. In these situations there is, of course, no possibility of the hybrid's crossing with either of the parent-species or of the formation of goneoclinic hybrids. *Nuphar intermedium* subsists independently there, multiplies without change of form, and has in fact established itself as a species. This phenomenon is explained as follows: The northern limit of

the distribution of each of the three Water-lilies in question is determined by their not being able to ripen fruits beyond that limit. Of the three, *Nuphar luteum* flowers the latest, and therefore its fruits are also the latest to ripen, whence it follows that it is the first to fall behind; that is to say, it reaches the northern limit of distribution sooner than the others, and ceases to ripen fruit in regions where the others are still able to do so. But *Nuphar pumilum* and *N. intermedium* are also different from one another in this respect. In Norbotten and Lapland *Nuphar intermedium* ripens its fruits a little earlier than *N. pumilum*, and it is consequently able to extend rather further north than *N. pumilum*. The further north plants go, the shorter becomes the time allotted for the performance of their annual work; and those which ripen their fruits early have a great advantage over those which ripen later. Concerning *Nuphar intermedium*, it has also been ascertained that the individual plants produced in nature are more fruitful than those reared in gardens from artificial crosses. In the case of plants obtained in this manner in the Botanic Gardens at Königsberg each capsule contained from 15 to 18 fertile seeds, whilst capsules ripened in the small lakes of the Black Forest contained from 38 to 63, and others taken from plants growing in Lapland contained from 41 to 72 such seeds. From these data we may infer, in the first place, that *N. intermedium* is most prolific in situations beyond the range of the parent-species; and, secondly, that it would be wrong to suppose that because a hybrid may be comparatively infertile or actually sterile in a particular locality, such infertility is a characteristic of the plant wherever it may occur.

As may be gathered from the above account of these three examples, the advantage which a hybrid may possess over the parent-species, whereby it is enabled to subsist and multiply side by side with those species, is not always of the same kind. In one case it is the more vivid coloration of the flowers, in another the fact of the hybrid being better adapted to a particular state of the ground, whilst in the third the earlier ripening of the fruits, which enables the hybrid to stand a more rigorous climate, gives the requisite advantage. These do not, of course, exhaust, by a long way, the possible sources of superiority, and there are many instances of hybrids which thrive better than the parent-species when the climate becomes milder, moister, or drier, as the case may be. It is obvious that of all the different advantages which may come into play those connected with climatic conditions are the most important, and the genesis of hybrids is probably most frequently due to the operation of this kind of advantage.

Far too little significance has been attached to the fact that the greater number of hybrids are not found in districts where the parent-species grow together with equal luxuriance, but occur where one or other of those species is meagrely represented, owing to the climate not being favourable to its distribution. Again, large numbers of hybrids are found in parts where the boundaries of several species coincide. In Europe such regions exist in the strips of land where the advance-posts of the Floras of the Baltic and Black Sea, and the Floras of the Baltic and the Mediterranean, respectively, encounter one another, and particularly in the

lower limits of the Alpine Flora. Another characteristic of these borderlands is the fact that the separate hybrids growing on them are almost always represented by a large number of individuals, and the consequence is that there is no great chance of their crossing with the parent-species and gradually reverting, in successive generations, to those species. If isolated individuals belonging to a particular hybrid grow in the midst of thousands of plants of the parent-stocks, their stigmas will, in all probability, be dusted with pollen from the latter species. This probability diminishes, however, as the number of individuals of the parent-species flowering in the same locality as the hybrid diminishes; if that number is small the hybrid is thrown mainly upon its own resources for fertilization, and, provided it is self-fertile, there is nothing to prevent its multiplying and becoming dispersed.

Connected with the above is the further fact that in the neighbourhood of a hybrid which has become a species there is sometimes no trace of one of the parent-species, it having completely died out. The slightest change in climatic conditions may cause the plants of a particular stock to succumb at the confines of the stock's area of distribution, where they are only present in small numbers, and are anything but strong; and when this happens we find the other parent-species alone growing side by side with the hybrid, and even that species is possibly not so well adapted as the hybrid to the altered conditions. Of cases in point we will select two from the East of Europe and two from the West.

When *Epilobium alsinefolium* and *Epilobium palustre* are crossed a hybrid is obtained which, when fertilized with its own pollen, yields a large quantity of fertile seeds. The plants reared from these seeds exhibit the same characteristics as the plant from which the seeds were taken. This hybrid grows together with the parent-species in the Riesengebirge, and has received the name of *Epilobium scaturiginum*. It is likewise a native of the Bihar Gebirge, on the confines of Hungary and Transylvania, and is of very common occurrence in the springs and rivulets in the vicinity of the Hochkamm (a mountain of this chain). Yet, of the two parent-species, only one, viz. *Epilobium palustre*, grows amongst these mountains. Again, *Prunella hybrida* is a hybrid springing from *Prunella laciniata* and *Prunella vulgaris*. It is widely distributed in the Wienerwald district, and in some places is commoner than the parent-species, whilst in Moravia and Bohemia it occurs in places where one of the latter, viz. *Prunella laciniata*, is entirely absent. A third instance is afforded by *Primula brevistyla*, called also *Primula variabilis*, a hybrid derived from *Primula vulgaris* and *P. officinalis*. This plant is true to seed, and is met with everywhere throughout almost the whole of Europe in company with both parent-species. In some districts of France it is found also in places where one or other of the latter species does not grow at all, and even where both are absent. Our fourth example, *Linaria stricta*, is the hybrid of *Linaria striata* and *Linaria vulgaris*. It occurs in many places in the West of Europe, together with its progenitors, but in the South of France, in the neighbourhood of Montpellier, it is found growing with *Linaria striata* alone, whilst the other parent-stock, *L. vulgaris*, is never found in the district.

We shall have another opportunity of describing the way in which the lines of demarcation of the ranges of entire floras become displaced in consequence of the changes which the climate of a region is liable to undergo in course of time. These displacements of floral regions are, as a rule, the result of very slow and inconspicuous migrations on the part of the plants constituting the floras in question. The direction of migration is invariably towards the places whose climatic conditions agree best with the organization of the plants, and is, in the case of any one species, either an advance or a retreat, according to the nature of the circumstances which impel the species to migrate. The different plants of a flora do not all migrate in a host together. Some species abandon their former home entirely and establish themselves in a new locality more or less remote from it; others leave a few of their kind behind in the old settlement at isolated spots which happen to be in peculiarly favourable situations, and many succumb to the effects of the new conditions or to the hardships incidental to the migration, and so die out. These changes in the range of floras are naturally accompanied by all sorts of alterations in the social relationships of the plants concerned especially with regard to the co-existence of hybrids and their progenitors. It may happen that one or both parent-species are left behind, whilst the hybrid advances, or the hybrid may remain behind, whilst one of the parent-species advances; or, again, one of the parent-stocks or both may die out. The facts concerning these local displacements explain the phenomenon that species which, from their characteristics, may be looked upon as hybrids of two other species, occupy in each case a district which is separated, and often at a considerable distance, from the areas inhabited by the species supposed to be their progenitors. The characteristics of the kind of Sorrel named *Rumex Patientia* lead one to the conclusion that it is a hybrid derived from *Rumex aquaticus* and *Rumex crispus*. It is found, however, growing wild in Hungary and in Bosnia in parts where neither *Rumex aquaticus* nor *R. crispus* occurs at all. In Herzegovina there grows fairly commonly a *Micromeria* which has been named by one of my friends *Micromeria Kerneri*. So far as its characteristics are concerned it must be considered to be a hybrid of *Micromeria graeca* and *Micromeria Juliana*; yet neither of these two species grows in Herzegovina at the present time, and they are not met with at any nearer spot than the part of Dalmatia which stretches westward from Herzegovina, and belongs to the area of distribution of the Mediterranean flora. In the little upland valleys of Planail and Plawen, which run down from the mountains of the Oetzthal into the valley of the Adige, there grows a Pulsatilla named *Putsatilla nutans*. If it occurred in company with *Pulsatilla vulgaris* and *Pulsatilla montana*, all Botanists would be unanimous in looking upon it as the product of a cross between those two species. Yet *Pulsatilla vulgaris* and *P. montana* do not grow in the high valleys in question, but are first met with at a distance of many miles from them, the former in the Unterinnthal and the latter in the Vintschgau (a portion of the Adige valley).

Inasmuch as the last-mentioned cases have to do with processes which have taken place long ago they partly belong to the next chapter, where the genesis of

species in the past will be discussed. They here bring to a natural conclusion a series of examples adduced to show in what manner a genesis of new species may ensue in the present, and may have taken place in the past. No sharp line of demarcation is to be found between different epochs in this connection any more than in the case of any of the other phenomena which, in the aggregate, constitute the history of species.

Now that it has been shown how new species arise from hybrids, or, in other words, from the crossing of species in pairs, the question presents itself whether, in addition to this one method, there are not also others leading to the same result. In answering this question we must bear in mind that every permanent change in external form which is inherited by a plant's descendants must be preceded by a change in the constitution of the protoplasm, and that so far as investigation has elicited the facts, the centre of the change is located exclusively in a particular protoplast which lies hidden in the ovary and there receives the spermatoplasm. The stimulus which causes the change in this protoplast can only proceed from the spermatoplasm, and every speculation concerning the formation of new species must therefore be associated with the question whether in the intercrossing of plants of one species and in autogamy the protoplasm in the course of its journey to the ooplasm may, as a result of its exposure to new external conditions, undergo modifications of so fundamental a kind that its influence on the ooplasm is subject to corresponding variations. In the first place, it might be imagined that the pollinated stigmas do not always act in the same way upon the spermatoplasm of the pollen-cell. Reference has already been made to the fact that a stigma may sometimes be almost simultaneously dusted with the pollen of very different plants (see p. 404), but that it has the power of exercising a selection, and that in every case only one kind of pollen is induced to put forth tubes by which a real fertilization is accomplished. The other kinds of pollen upon the stigma are not known to have a direct effect upon the ovule. But that there is some interaction between them and the protoplasm in the cells of the stigma is evidenced by the fact that they swell up wherever they are in contact, and (as has been shown, p. 414) are frequently found developing pollen-tubes. Now it is possible that the reciprocal action of the contents of these pollen-cells and the contents of the stigmatic cells may produce some change in the latter, which is transmitted to the contents of those other pollen-tubes which are to enter into combination with the ooplasm. Such modification might conceivably affect the nature of the stimulus imparted to the ooplasm, and this alteration in the stimulus might be manifested in a change in the form of the individual arising from the fertilized ooplasm. The likelihood of all these possibilities and assumptions being satisfied is extremely small, but as no researches have yet been instituted into the matter, it cannot be dismissed with an unconditional negative.

In artificial crosses between different species of *Cirsium* it has often been noticed that pollen-cells taken from a single capitulum vary in their effects upon the stigmas of a second capitulum, inasmuch as the seeds produced by the different florets, though all fertilized with the same kind of pollen, yield dissimilar plants when

they germinate. The variation is limited, it is true, to the different degrees in which the seedlings resemble one or other of the parent-plants. If the cross is between two plants of the same species no such variation can occur, seeing that the plants crossed are alike in form. But there is still the question whether differences in the age, size, and luxuriance of growth of the individuals which cross may not have some influence on the result. So far as my experiments show, these differences have no effect on the genesis of new forms, and have no prospect of becoming permanent characters in the offspring. A poor stunted plant growing on dry soil may produce seeds which, on being planted in a good moist soil give rise, under favourable conditions, to well-developed plants capable of flowering luxuriantly. As is well known, the first flowers of an inflorescence are always much larger than those which subsequently open at the apices of the spike or raceme, or on the ultimate ramifications of the cyme as the case may be. Now, if the large earliest flowers are crossed one with another, and likewise the small latest flowers, and the seeds so obtained in each case are kept separate but reared under similar conditions, the plants produced from them do not differ in the slightest degree from one another, but in their turn bear flowers, of which the first are the largest and the last the smallest. Notwithstanding these results, however, I should not like, without further investigation, to deny the possibility of the specific constitution of the spermatoplasm undergoing some change as a result of external influences in the course of its development, whether during its imprisonment in anthers or antheridia or on its way to the ooplasm, or to say such change might not cause the descendants of the plants concerned to differ in form from the individual from which they sprang.

It has been established beyond all doubt that modifications of form directly induced by conditions of soil or climate are not hereditary, and that every change of form which persists in the descendants is only brought about as the result of a process of fertilization, or, in other words, that new species can only arise through fertilization. Herein lies also the solution of the marvellous phenomenon known as the alternation of generations, and of the question why plants in general flower and undergo fertilization. To these processes is due the genesis of new species. The propagation of plants, their multiplication and dispersal, may also be effected by means of brood-bodies, and as a matter of fact these processes are continuously operating on a vast scale. But the plants reproduced by brood-bodies retain the form of their ancestors unaltered, and no new forms arise in this way. Suppose that a locality is occupied exclusively by plants which multiply by brood-bodies only and do not change their form, and that in consequence of a change in the climate such species as are not adapted to the new conditions abandon their homes, or else languish and die out, the probability is that many of the vacated spots will remain unoccupied owing to there being no recruits in the neighbourhood, or from out its confines, that are better adapted to the new conditions. If, on the other hand, the area in question is inhabited by plants which reproduce sexually and which, by crossing one with another, produce descendants of diverse forms, there is

every probability that amongst the assemblage of new forms some will be better adapted to the new conditions when a change of climate occurs than those of the old species which are driven out thereby, and that these new forms will therefore be able to take the place of the latter.

It is only from this standpoint that we can properly understand the phenomena of the alternation of generations, the separation of the sexes, dichogamy, and all the rest of the wonderful floral contrivances, the object of which is to facilitate the crossing of two species during the first stage of flowering and only to allow of crossing between plants of one species, or of geitonogamy, autogamy, or cleistogamy in the event of no inter-specific crossing taking place. As a result of these contrivances, numberless new forms are continually being generated which are respectively adapted to all the most various conditions of soil and climate. So long as no change in climatic conditions takes place, the majority of these forms have very little chance of surviving and of naturalizing themselves as species amongst the plants already established in the same locality. But when, in consequence of a change of climate, the ranks of the species in possession of the ground are thinned through the abdication of many of those best adapted to the conditions of life previously existing, the real significance of the new forms which have arisen as a result of the sexual process is manifested in the fact of those which are best adapted to the new conditions taking possession of the spots vacated and settling down there as new species.

DERIVATION OF EXISTING SPECIES.

The plants preserved as fossils in former ages are not only the forerunners but the ancestors of the existing vegetation of to-day. There was no general rejuvenescence and extinction of organisms coincident with the beginning and end of the several "periods" of the history of the earth. The changes in the organic world, like those in the inorganic crust of the earth, were accomplished gradually by slow degrees, and the organisms of the present day are a continuation of, and have been slowly evolved from, those of former ages.

So far, there is little difference of opinion amongst naturalists; but as to the causes of the differences in form between the vegetation of the present and the past, the most various theories are held. Nor is this surprising, seeing how largely our conclusions are based on conjectures. And when the flood-gates of speculation are rolled back it is not always that the proven is clearly distinguished from the unproven. An import is attached to isolated facts which they do not merit, and—most mischievous of all—the existence of wide lacunæ in our knowledge is concealed, or these lacunæ are dexterously bridged over with unmeaning, high-sounding words and hollow phrases which, while astonishing us for the moment, leave us chastened and confounded. The confirmed mistrust aroused by these extravagances which obtains concerning all that bears on the derivation of species demands that we should devote a brief consideration to the prevailing theories, and especially to

such as bear upon the conversion of species of former times into those of the existing vegetation.

A change in the conditions of life has, according to a widely-spread view, been the immediate cause of a change in the vegetation. The altered conditions of life provoke new wants in the plant, and these new requirements have led to a transformation of their organs. Stimulated by use, the organs in question become enlarged and further developed; others, no longer of service, become smaller, atrophy, and disappear. It is the cumulative result of these small and almost imperceptible changes that in course of time becomes apparent. These structural changes are transmitted to the progeny, and with an increasing tenacity, the greater the number of generations which have been exposed to the altered conditions. This, the *theory of adaptations*, has provoked wide discussion and criticism. It is urged against it that, whether wild or cultivated plants be considered, it is only isolated or a few individuals, never the whole of the members of a species, which exhibit these variations and transmit them to their offspring. If these new characters are immediately due to the soil or climate, then all the individuals of a species, exposed to like conditions of growth (environment), should exhibit them and hand them on to their offspring. The permanence of the influence—and to this many naturalists and others attach great importance—is without significance in this matter. When a change is called forth—be it by an altered source of nourishment, by the influence of heat or cold, light or darkness, moisture or dryness—it must become apparent upon the growing plant, since a change in the plant stands to a change in the environment as effect to cause. If the cause ceases, so also does the effect, equally after the lapse of a year or a hundred years. But a much more potent criticism of the theory of adaptation is the result of a series of experiments which were carried out for the solution of these questions. From them we see that an altered environment calls forth certain changes in the plants submitted to it, but that these are not transmitted to the offspring, are not hereditary, and that the influences of soil and climate do not provoke a fundamental change in the constitution of the protoplasm. Influences of this sort can induce a diseased condition in a plant and can even kill it, but they cannot bring about a change which can be transmitted to the next generation. Though soil and climate play a most important part in the struggle of species and varieties for existence, and though the environment has a great influence on the origin of varieties and on the distribution and migration of plants—as the immediate stimulus to the origin of new and transmissible characters, and thus to the modification of species, change of environment is without significance.

Another theory dealing with the origin and modification of species is that known as the *theory of progressive transformation by inherent forces*. According to it, the impulse to change resides in the inherent tendency of all species to perfect themselves. This theory transcends all experience and depends on premises and draws conclusions essentially metaphysical in nature; it deals only in part with the results of scientific observation. It presupposes a creation of living

protoplasts endowed with the capacity to alter their constitution on their own initiative; and, further, that these alterations take place along predetermined lines in a direction leading from a lower to a higher platform; consequently the imperfect organism necessarily, in course of time, passes over into a highly developed, perfect one. Against this theory the following may be urged: The first assumption involves creation. The question is: Is it possible for a living protoplast to be formed from inorganic matter without the co-operation of already existing living beings? The question obviously concerns the present and future as well as the past, for what has happened once may again take place, for the forces of nature, according to the laws of the conservation of matter and energy, remain the same for all time. The discussion of this question resolves itself into this: whether a little bit of protoplasm can arise from inorganic matter, and after its origin can acquire the capacity of growing by the absorption of food from its environment, &c.; in a word, whether it can exhibit those changes and movements which we term life. When first organic compounds (formic acid, urea, sugar, &c.) were synthesized in chemical laboratories from inorganic substances like ammonia, carbonic acid, and water—compounds which formerly had only been produced as a result of the activity of living protoplasm—naturalists began to think that these things might take place in nature independent of already existing plants. It seemed possible that these substances might, under the uncontrolled forces of nature, unite and arrange themselves in the same manner as occurs within a vegetable cell. The tendency of matter to combine, which plays so important a part in nature, was pointed out, and especially the similarity between the structure of crystals and that of certain cells; the properties of finely-divided soil also were called to mind, how it absorbed gases, took up water in varying quantities, altered salt-solutions, separating certain of their constituents, and what was especially noteworthy, increased the capacity of many simple substances to combine. This was at a time when chief importance was attached to the chemical properties of protoplasm; it was thought that, once given the substance, it would form itself into cells like crystals. Of the ultimate structure of protoplasm and of the nucleus knowledge was as yet very incomplete. The tendency of that time was to explain all those phenomena which constitute life as the resultant of the various forces which form inorganic bodies, and to deny the existence of any wide gulf between the living and non-living world.

The experiments to produce living matter had all of them negative results. But this of course is no proof of its impossibility; for it can always be urged that wrong methods were followed, and improper conditions imposed. Nor, on the other hand, does it follow from the fact that hitherto living matter has never been known to originate independently of existing organisms, that its production is impossible. Since we cannot arrive at definite results by experiment, the investigator must depend on other considerations.

The second assumption of the theory of transformation from internal causes, that plants have the inherent capacity to modify their internal constitution and,

similarly, their external form spontaneously, has been so fully met by the observations recorded in the last chapter that it is hardly necessary to deal with it now at great length. I shall content myself with pointing out that it is impossible to give a natural explanation of such a phenomenon. Every variation presupposes a corresponding disturbance; for the acquirement of any new structural character the plan of construction must undergo some fundamental alteration. The naturalist is unable to grapple with the phrases "internal causes", "internal force", "force of transformation", "tendency to differentiate", "principle of progressive transformation", when attempting to explain variation in a natural manner upon mechanical principles. Nor is the likening of this transformation to the metamorphosis which every individual passes through at various periods of its existence at all to the point, since metamorphosis repeats itself with great constancy in every species according to the plan of construction which is laid down in the specific constitution of the protoplasm. That the protoplasm of any species should, in the absence of any impulse or stimulus from outside, be able spontaneously to alter its plan of construction contradicts all our experience of the normal action of natural forces. Even should we conceive vital force, the dormant energy of the protoplasm, to be converted into an active form, it could only give rise to movements which have their origin in the specific constitution of the protoplasm.

And now we come to the assumption that this inherent force of transformation is a progressive one, that it leads to a higher or more perfect development. But what is to be regarded as a higher development amongst plants? A tree with its brightly coloured flowers and luscious fruits seems more highly developed to the non-botanist than a low herb with inconspicuous flowers, or than the green filaments of a Spirogyra destitute of flowers. The supporters of the theory under discussion assert that the highest development is that which exhibits the greatest complexity of form, and in which division of labour is carried furthest. And in this assertion they do not essentially differ from the popular view. Complexity of form and division of labour are undoubtedly carried further in an Apple-tree than in the Spirogyra of the ponds and ditches. But it must not be forgotten that the differentiation of a plant-body into various tissues, the production of wood, bast, and cork in its stem, of cuticle, stomates, and hairs on its leaves, of various colouring-matters and aromatic substances in its petals, and of sweet juices in its fruits, stands in harmonious relation to the environment of the plant in question. Change the conditions, and imagine the Apple-tree submerged in a pond; it is no longer in harmony with its surroundings, its complexity of tissues, its wood, stomates, &c., are not so well adapted for these conditions as are the Spirogyras and Water-weeds equipped with organs of another type. The size of a plant is often—in the popular estimate—the indication of its high organization. A big plant gives the impression of possessing a more perfect development than a small one. But this criterion leads to no satisfactory result; it is sufficient to instance the case of certain huge sea-weeds (*Macrocystis*) of the southern seas, which exceed our greatest forest trees in height. Many Thallophytes, only visible under

the microscope, show a greater complexity of structure of their constituent cells than do many Flowering Plants; and, should especial importance be attached to this character, Diatoms and Desmids must be regarded as more highly organized than many small annual Composites. The idea of progressive development implies a recognition of that species of plant which is most highly developed and which stands upon the apex of the pyramid, or, at any rate, of the group of plants which has already reached the furthest point—is it the Aristolochiaceæ, Cannaceæ, Magnoliaceæ, the Orchids, the Composites, the Ranunculaceæ, the Papilionaceæ, or the Pomegranates? Any one who has studied carefully the structure of these plants knows well that it is impossible to make an estimate of this kind. In a book of Botany one group must be treated first and another last, but this does not necessarily imply that the last is the most highly developed; indeed the various writers of systematic works begin and end with the most various groups. Like the theory of adaptability, that of progressive transformations from inherent forces fails to give us a reasonable explanation of the variations which plants have undergone in process of time.

A third theory, based on the observations of modern times, is as follows: That variations of form in the offspring arise through crossing, from the union of two dissimilar protoplasts. This theory, based on the union of unlike forms, has been fully sketched out in the last chapter. It assumes the existence in former times of a vegetation rich in forms—an assumption amply justified by the fossil remains which have been preserved. New forms arose, not by a progressive development such as has been alluded to, but by a transformation or metamorphosis of those already in existence. It was from the union of existent types that incipient new species were produced. By the periodic recurrence of changes in climatic conditions the areas of plant-distribution have received continual displacements, and it was then that these incipient species or varieties were put to the test. Those well-suited to the fresh conditions settled down into new species. They replaced their less well-adapted ancestors in the plant-community, and they played the same part as these had formerly done. A change indeed is brought about; but not (on the lines of the theory of adaptability) as a direct result of climatic influences, nor from an inherent tendency to progressive development. It arises rather from a change in the specific constitution of the protoplasm in consequence of the crossing of unlike forms. In basing the transformation of species on a crossing of this nature we are relieved the necessity of picturing lacunæ in a vegetation as a result of climatic changes, or of any serious disturbance of the inter-relations of its various component forms. Bacteria and Moulds, Mosses and Lichens, Ferns, Grasses, Palms, and Coniferous Trees, have all of them a special function to fulfil in the great community of plants, and they are to a certain degree dependent on one another. Were one removed the whole would be affected, and it might well happen, did a given group come to speedy extinction, that the whole community of plants might suffer. But in every group at all times and in all places a reserve of new forms continually arises by crossing, so that this danger is averted. With climatic

changes, of the older, less fit forms some are extinguished, whilst young, new forms step into their places. Thus we see also that the conversion of Mosses into Ferns, of Ferns into Conifers, and of Grasses into Pinks, &c., as assumed by the theory of progressive transformation, would be a positive disadvantage to plants as a community, and that its tendency would be in the direction of anything but real progress.

It is important to recognize the fact that in the production of new forms by crossing, it is not especially such forms as are constituted to resist an anticipated change of climate that are produced. Of the forms which arise, some are fitted for a more inhospitable, others for a milder climate; but it cannot be said of any that they possess an assured future. Such only are able to maintain, propagate, and establish themselves, as are from their internal organization and external form in harmony with the prevailing climatic conditions of the moment. Those so constituted that they are unable to thrive under the given external conditions linger and become extinct; they are outstripped and overgrown by such as find the environment to their liking. Hence we speak of the struggle for existence. Plants in harmony with their surroundings are the victors, and they establish themselves upon the arena of this encounter. This, briefly, is Darwin's theory of Natural Selection, a theory which marks an advance upon all other theories of the origin of new species. Though many views may be held as to the precise manner of origin and transformation of forms, there can be no difference of opinion as to the significance of the struggle for existence and of the survival in this struggle of those forms best fitted by their organization to the circumstances of the environment.

THE SUBDIVISIONS OF THE VEGETABLE KINGDOM.

The fact that the savants of ancient times made no attempt to classify plants according to their structural characters is explained by their limited botanical knowledge. Their interest was restricted to such plants as were in use as drugs, poisons, and charms, to vegetables, fruits, and cereals, finally, to such as were of value for decorative purposes and as symbols of religious observances. Nor was the number of these plants considerable. Some five hundred forms were known to Theophrastus (300 B.C.), whilst Pliny (23–79 A.D.) records about twice that number. The characters of these few plants could be retained in the memory for the purposes of comparative investigations, and their recognition depended in large part upon the general impression gained in the ordinary intercourse with nature. Enumerations of plants were based far more on their medicinal or economic uses, on their hurtfulness and beneficence for mankind, than on any structural characters they might possess in common. Even in the herbals of the sixteenth century, containing, as they did, new descriptions and incomparable woodcuts, were the medicinal and economic properties of the various plants still especially emphasized; Botany was still almost exclusively the handmaiden of medicine and agriculture.

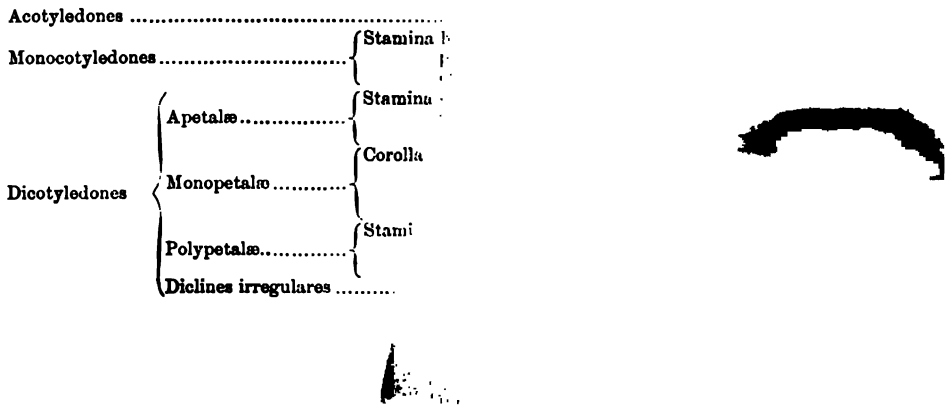
The first botanical writer to break with these old traditions was Clusius (1526–1609); he described plants as he observed them, quite apart from their value to man. Clusius, though a Belgian, spent many years of his life at Vienna, and thoroughly explored the Flora of Austro-Hungary; previously he had investigated the plants of Spain and Portugal. To England he paid more than one visit, and received many exotic plants from Sir Francis Drake, the voyager. In his *Rariorum Plantarum Historia*, published originally in 1576, we find the first attempt to classify plants according to their similar characters. In separate books he deals with trees, shrubs, and under-shrubs, bulbous plants, sweet-smelling flowers, scentless flowers, poisonous, narcotic, and acrid plants, with plants having a milky juice, and with Umbellifers, Ferns, Grasses, Leguminosæ, and certain Cryptogamic plants. In those days some 4000 plants were distinguished by Botanists, and the want of some system of classification was gradually felt. The groups of Clusius and his contemporaries were inadequate, and the system of Cesalpino (1519–1603), published in the first book of his *De Plantis Libri XVI* (1583), failed to obtain the recognition it undoubtedly deserved—perhaps because it was only sketched out in outline and lacked a full and detailed rendering. Cesalpino was the first to convert observation into real scientific research; he drew attention to the more hidden organs of plants, to the position of the seeds, the number and mode of insertion of the cotyledons, &c., to the presence or absence of flowers.

It is to Tournefort (1656–1708), a Frenchman, that we owe the first complete review of known plants in synoptical form. In his *Institutiones Rei Herbariæ* (published 1700) 10,146 species of plants are distinguished and arranged in 698 genera, which again are assembled under 22 classes. Classes 1–15 include herbs and under-shrubs, 16 and 17 flowerless plants (Cryptogams), and 18–22 shrubs and trees. The herbs, shrubs, and trees are distinguished by the form of their flowers, especial importance being attached to the presence of calyx and corolla, to the regularity or irregularity of the flower, and to the petals—whether they are free or united with one another. Not long afterwards Linnæus produced a classification of plants based on the distribution of the sexes, and especially upon the number of the stamens in the flowers. The terms species and variety, genus and class, were more clearly and intelligibly defined than heretofore, and his 1050 genera were included under the 24 classes already enumerated (p. 288). The Linnean classification, known as the Sexual System, enjoyed an unprecedented recognition. It constituted a well-arranged summary of a great mass of scattered observations, and made it possible for species to be identified by means of concise descriptions. It was not the fault of this accomplished and renowned naturalist that a greater importance were attached to his system than he himself ever intended. Linnæus never regarded these 24 classes as real and natural branches of the vegetable kingdom, and expressly says so; it was constructed for convenience of reference and identification of species. A real natural system, founded on the true affinities of plants as indicated by their structural characters, he regarded

as the highest aim of botanical endeavour. He never completed a natural system leaving only a fragment (published 1738).

The credit of actually founding a natural system of plants is usually attributed to Bernard de Jussieu (1699–1777) and his nephew Antoine Laurent de Jussieu (1748–1836). For many years this system only found expression in the laying out of the beds in the Botanic Garden of Trianon (at Versailles); it first became generally known some thirty years after its inception, when the younger de Jussieu published his *Genera Plantarum* (1789). A hundred families of plants are distinguished and grouped under fifteen classes, which, in their turn, fall under three main co-ordinated divisions (Acotyledones, Monocotyledones, Dicotyledones). The three main divisions[1] are founded upon the structure of the embryo at germination. In the Acotyledones the embryo consists of a single cell and is destitute of cotyledons, in the Monocotyledones it is cylindrical and provided with one cotyledon, whilst in Dicotyledones there are two. The Acotyledones are equivalent to the Cryptogamia of Linnæus (*cf.* p. 290) and constitute the 1st class of the new system. The Monocotyledons fall into three classes according to the relative position of stamens to ovary (Monohypogynæ, Monoperigynæ, Monoepigynæ). The Dicotyledons are first subdivided into three groups according to the nature of the corolla, viz., into those destitute of petals (Apetalæ); those with a gamopetalous corolla, the petals being united (Monopetalæ); and those with a polypetalous corolla, with all the petals free from one another (Polypetalæ). These are each subdivided into three classes, based on the relative position of stamens to ovary (in the case of the Monopetalæ of corolla to ovary), but as plants with unisexual flowers it was impossible to bring into relation with stamens and ovaries, a special class (Diclines irregulares) was added. The institution of this last class does not redound to the credit of the system; whilst the limitations of the other classes, based on the relation of stamens to ovary is cumbrous and unnatural, as compared with those of the Linnean Sexual System. The characters upon which de Jussieu are the broad characters upon which the division is based, the structure of the plant being taken into consideration of Monocotyledons and Dicotyledons.

[1] A. L. DE JUSSIEU'S



Plants. A. P. De Ca… …ng to the characters of the *ou Exposition des* … …ale (= Monopetalæ), and Poly- tinguished between … …l to be an unnatural one, it is former are construc… …families belonging to the great met with. The cellular … …relations to one another. An lares aphyllæ) and … …families have been developed one vascular plants were … …arrangement in linear series is as time into those in which … …branches. Very appropriate was and were supposed to … …hose families with the dovetailing of the vascular bundles … …mily stands in touch with two, another (Exogenæ). The group … …allied families. This contact or rela- cryptogamæ), forms … …families are extremely large and (Endogenæ phanerogam… …as it were, jammed in between them; ledones, were divided … …e coast of a continent. those with a distinct … …m of Alexander Braun,[1] published in subdivided into three … …randenburg. Though the division of into a continuous co… …and Eleutheropetalæ suggests at first sight the calyx; and the T… …icher, there is a difference, and an important the floral receptacle … …luded by the older Botanists in the Apetalæ essentially different … …alæ. With the Eleutheropetalæ are ranked there are many de… …olla are typically present, the latter consisting on the whole an agre… …ranged in 24 Alliances or Cohorts—Hydropeltidinæ, note the recognition … …etales, Passiflorinæ, Guttiferæ, Lamprophyllæ, Hes- mames) as the two … …, Terebinthinæ, Gruinales, Columniferæ, Urticinæ, thus the Cellular … …Saxifraginæ, Julifloræ, Umbellifloræ, Myrtifloræ, Thy- one another. The … …oræ, Leguminosæ. In recent times we have the systems cotyledons and Di… …They follow the lines laid down by Alexander Braun, but, onwards in all lat… …ther, the group Apetalæ (or Monochlamydeæ) is entirely no constitute so … …being referred in part to the Sympetalæ, and in part to the are all more nearly … …chichlamydeæ of Engler). other groups.

Following De … …fifty years our knowledge of the Cryptogams constituting the during the first … …(founded by Endlicher, *cf.* foot-note, p. 604) has increased by Agardh, Martius … …Several attempts have been made to bring together the results the non-botanic… …earches upon this group, and to utilize them for classificatory

[1] ALEXANDER BRAUN'S SYSTEM.

I. VASCULAR … (Algæ, Lichens, and Fungi).
2. … …odes (Characeæ, Mosses, and
3. … …worts).

… …Equisetums).
… …s).

III. ANTHOPHYTA (Flowering Plants).
A. GYMNOSPERMÆ (seeds exposed).
1. Frondosæ (Cycads).
2. Acerosæ (Conifers).
B. ANGIOSPERMÆ (seeds in an ovary).
1. Monocotyledones.
2. Dicotyledones.
a. Apetalæ.
b. Sympetalæ.
c. Eleutheropetalæ.

of plants, this great variety of specialist opinion is somewhat surprising, and tends to shake his confidence in all botanical systems. But it must be remembered that in the development of a natural system the imagination plays a much more important part than in the elaboration of an artificial one, nor can prevailing currents of thought, or the particular habit of mind of the observer, be without their influence. Very prominently does this appear in the case of the Botanists who came under the influence of what has been termed nature-philosophy during the early portion of this century. Thus Reichenbach and Oken proposed systems which can only appear to us absurd; but it would be wearisome and useless to follow their absurdities in detail.

The system of classification proposed by Endlicher[1] (1805–1849), and published in his *Genera Plantarum secundum ordines Naturales disposita* (published 1836-1840) is based on the systems of de Jussieu and De Candolle. In it 6838 genera, arranged in 277 families or orders, are included. Here for the first time are the Coniferæ and Gnetaceæ distinguished as a special group, and designated as Gymnosperms. Here also is that group of cellular plants known as the Thallophyta carefully distinguished into three series, the Algæ, Lichens, and Fungi. But we still find these groups treated as equivalent to the Horse-tails, Ferns, Lycopods, &c.; so also with the Gymnosperms, they are not treated as a distinct subdivision, but only as a class of Dicotyledons (Acramphibrya), the other classes of which are the Apetala, Gamopetala (= Monopetalæ), and Dialypetala (= Polypetalæ).

In fairly recent times Bentham and Hooker,[2] in their well-known *Genera Plantarum* (published 1862–1883), follow essentially the systems of De Candolle and Endlicher. They assemble all flowering plants (100,220 species) into 8417 genera, and these under 210 families or orders. Of these orders 3 belong to the Gymnosperms, 35 to the Monocotyledons, 36 to the Monochlamydeæ, 46 to the Gamopetalæ, and 90 to the Polypetalæ.

[1] ENDLICHER'S SYSTEM.

I. THALLOPHYTA (no opposition of stem and root).
- PROTOPHYTA.
  - Algæ.
  - Lichenes.
- HYSTEROPHYTA.
  - Fungi.

II. CORMOPHYTA (opposition of stem and root).
- ACROBRYA (stem growing at the point only).
  - Anophyta (Liverworts and Mosses).
  - Protophyta (Vascular Cryptogams and Cycads).
  - Hysterophyta (certain parasites, Balanophoreæ, Rafflesiaceæ, &c.).

II. CORMOPHYTA—*Continued.*
- AMPHIBRYA (stem growing at the circumference).
  - Includes Monocotyledons.
- ACRAMPHIBRYA (stem growing at both point and circumference).
  - Gymnosperms (ovules naked, fertilised directly from the micropyle).
  - Apetala (Perianth 0, rudim. or simple).
  - Gamopetala (Perianth double, petals united).
  - Dialypetala (Perianth double, petals free).

[2] THE MAIN DIVISIONS OF BENTHAM AND HOOKER'S SYSTEM (FOR FLOWERING PLANTS ONLY).

- DICOTYLEDONES.
  - Polypetalæ.
  - Gamopetalæ.
- DICOTYLEDONES—*Continued.*
  - Monochlamydeæ.
  - Gymnospermæ.
- MONOCOTYLEDONES.

Though the grouping of Dicotyledons (according to the characters of the perianth) into Monochlamydeæ (= Apetalæ), Gamopetalæ (= Monopetalæ), and Polypetalæ (= Dialypetalæ), is very generally recognized to be an unnatural one, it is no easy task to replace it by a better one. The families belonging to the great group Dicotyledons show the most multifarious relations to one another. An arrangement, based on the assumption that these families have been developed one from another, is not discoverable; whilst an arrangement in linear series is as unnatural as one resembling a tree with its branches. Very appropriate was Linnæus's comparison of the limitations of these families with the dovetailing of the frontiers of countries on a map. One family stands in touch with two, another with three, others again with four or more allied families. This contact or relationship occurs on the most various sides. Some families are extremely large and comprehensive, others relatively small, and, as it were, jammed in between them; whilst others resemble scattered islands off the coast of a continent.

Well worthy of consideration is the system of Alexander Braun,[1] published in 1864 in Ascherson's *Flora der Provinz Brandenburg*. Though the division of Dicotyledons into Apetalæ, Sympetalæ, and Eleutheropetalæ suggests at first sight the classifications of de Jussieu and Endlicher, there is a difference, and an important one. A large number of the families included by the older Botanists in the Apetalæ are here placed in the Eleutheropetalæ. With the Eleutheropetalæ are ranked those plants "in which calyx and corolla are typically present, the latter consisting of separate petals". They are ranged in 24 Alliances or Cohorts—Hydropeltidinæ, Polycarpicæ, Rhœadinæ, Parietales, Passiflorinæ, Guttiferæ, Lamprophyllæ, Hesperides, Frangulinæ, Æsculinæ, Terebinthinæ, Gruinales, Columniferæ, Urticinæ, Iricoccæ, Caryophyllinæ, Saxifraginæ, Julifloræ, Umbellifloræ, Myrtifloræ, Thymelæinæ, Santalinæ, Rosifloræ, Leguminosæ. In recent times we have the systems of Eichler and Engler. They follow the lines laid down by Alexander Braun, but, carrying his method further, the group Apetalæ (or Monochlamydeæ) is entirely abolished, its members being referred in part to the Sympetalæ, and in part to the Eleutheropetalæ (= Archichlamydeæ of Engler).

During the last fifty years our knowledge of the Cryptogams constituting the group Thallophyta (founded by Endlicher, *cf.* foot-note, p. 604) has increased by leaps and bounds. Several attempts have been made to bring together the results of the various researches upon this group, and to utilize them for classificatory

[1] ALEXANDER BRAUN'S SYSTEM.

I. BRYOPHYTA.
1. Thallodeæ (Algæ, Lichens, and Fungi).
2. Thallophyllodeæ (Characeæ, Mosses, and Liverworts).

II. CORMOPHYTA.
1. Phyllopterides (Ferns and Equisetums).
2. Maschalopterides (Lycopods).
3. Hydropterides (Rhizocarps).

III. ANTHOPHYTA (Flowering Plants).
A. GYMNOSPERMÆ (seeds exposed).
1. Frondosæ (Cycads).
2. Acerosæ (Conifers).
B. ANGIOSPERMÆ (seeds in an ovary).
1. Monocotyledones.
2. Dicotyledones.
a. Apetalæ.
b. Sympetalæ.
c. Eleutheropetalæ.

purposes. The old division into Algæ, Fungi, and Lichens, based on the presence or absence of chlorophyll and on the mode of life of the forms in question, has been by many authors abandoned. Cohn in 1872 divided the Thallophytes, according to their methods of reproduction, into seven groups: Schizosporeæ, Zygosporeæ, Basidiosporeæ, Ascosporeæ, Tetrasporeæ, Zoosporeæ, and Oosporeæ. Sachs, in 1874, following somewhat similar lines, made four classes: Protophyta, Zygosporeæ, Oosporeæ, and Carposporeæ, in each of which groups both chlorophyll-containing (Algæ) and colourless forms (Fungi) occur, as may be seen by a perusal of the classification quoted below.[1] Gœbel (1882) returns in part to the older method and distinguishes between Algæ and Fungi; but with these as groups of equal systematic importance he ranks the Myxomycetes, Diatomaceæ, and Schizophyta. The Algæ he divides into Chlorophyceæ (Green Algæ), Phæophyceæ (Brown Algæ), and Rhodophyceæ (Red Sea-weeds); and the Fungi into Chytridiaceæ, Ustilagineæ, Phycomycetes, Ascomycetes, Æcidiomycetes, Basidiomycetes. Warming (1884) returns completely to the older method, dividing the Thallophytes into Algæ and Fungi, ranking the Myxomycetes with the Fungi, and the Diatoms and Schizophyceæ with the Algæ. The balance of opinion at the present time, largely swayed by the views and researches of Brefeld upon the Fungi, favours a grouping of the bulk of Thallophytes into Algæ and Fungi. Brefeld regards the various families of Fungi as more intimately related amongst themselves than are these families to corresponding families of Algæ. That Fungi have arisen from Algæ at some remote period, and have then amongst themselves undergone development along various lines, is very generally held; but the view that the different families of Fungi stand in near relationship to the several algal groups—as indicated, for instance, in the system of Sachs, (*cf.* foot-note below)—is not at present the prevalent one. And amongst the Algæ, also, the attempt to classify the various forms into families according to the relative simplicity or complexity of their organs of reproduction (as Sachs suggested) no longer finds general favour. Amongst the Algæ we find a number of extensive

[1] SACHS'S CLASSIFICATION OF THALLOPHYTES.

I. PROTOPHYTA.

Containing Chlorophyll.	*Not containing Chlorophyll.*
Cyanophyceæ.	Schizomycetes.
Palmellaceæ (in part).	Saccharomycetes.

II. ZYGOSPOREÆ.

Conjugating Cells Motile.

Pandorineæ (Hydrodictyeæ).	Myxomycetes.

Conjugating Cells Stationary.

Conjugatæ.	Zygomycetes.

III. OOSPOREÆ.

Sphæroplea.	
Vaucheria ... ... (*Cœloblastæ*), ...	Saprolegnieæ. Peronosporeæ.
Volvocineæ.	
Œdogoneæ.	
Fucoideæ.	

IV. CARPOSPOREÆ.

Coleochæteæ.	Ascomycetes (including Lichens).
Florideæ.	Æcidiomycetes (Uredineæ).
Characeæ.	Basidiomycetes.

groups, within the limits of each of which all stages of complexity in reproduction occur. The attempt to string together forms agreeing in reproductive methods makes it necessary to break up groups which on general grounds seem to be natural families. And as it is a natural system that we are striving after, systems like that of Sachs (which may be compared to the artificial sexual system of Linnæus) must be abandoned. That the publication of the Sachsian system in his widely-read "Text-book" has done great service to Botany there can be no doubt; it has stimulated thought and observation, and has led more speedily than would otherwise have been the case to the establishment of broad and probably sound views as to the relations of the Thallophytes. However, the Myxomycetes, approaching as they do certain groups of the animal kingdom, are kept apart from the rest of the Thallophytes in the most recent system.

The classification of plants according to their similarity of structure—species into genera, genera into families or orders, families into alliances or cohorts, these into classes, and classes into two chief branches or phyla, the Cryptogams and Phanerogams—leads to the presumption that these two chief branches have arisen from a common stock, have diverged from a common stem. A consideration of all animal and plant forms similarly leads us to the belief that the main stems of the Animal and Vegetable Kingdoms, respectively, meet at their points of origin. By studying systems of classification drawn up on paper and restricted to two dimensions of space, we involuntarily conceive the classes and orders of the vegetable kingdom, as a tree which continually branches, finally ending in thousands of twigs which represent the various species. Such is, rightly or wrongly, the conception of all Botanists who have concerned themselves with the construction of a natural system. They only differ in so far that some regard the Thallophytes as standing at the base, and derive from these the Liverworts and Mosses, from these the Ferns, &c., and so on to the Gymnosperms and Angiosperms; whilst others make a subdivision of the main trunk at once into Cryptogams and Phanerogams, each of these continually branching according to the various classes and families. Others again, whilst conceiving the whole vegetable kingdom as having a common origin, regard this as the centre of a sphere, and that the several phyla and classes radiate out from this, producing numerous branches and twigs at the surface of the sphere. Each of these hypotheses presupposes, in the first instance, the existence (or spontaneous generation) of a few Thallophytes of extremely simple structure which have become differentiated, *i.e.* given rise to more complex offspring which form the beginnings of the branches of the tree. To this kind of development of a tree-structure, the terms Phylogenesis or Phylogeny (from φυλή, a tribe; and γεννάω, to produce) is given. Obviously, not only the original forms possess the capacity of differentiating, but their offspring also, and so on through the entire tree. But views are divided as to whether this continued differentiation follows a predetermined plan, is due to definite inherent forces, or whether it may not be restricted in this sense and due to other and external causes.

That a natural system has been evolved along lines resembling the ramifications of a tree, which commenced with simply organized structures and terminated with the most complex ones, finds a certain confirmation when the history of development of the individual (ontogeny, from ὤν, ὄντος, being; and γεννάω, to produce) is compared with its position upon the phylogenetic tree. As we know, the greatest of all flowering trees begins its existence as a single protoplasmic mass. This surrounds itself with a cell-wall and increases in size and complexity at the expense of nutriment derived from its environment. Gradually cells and tissues arise and the young organism becomes segmented into an axis and appendages. These, again, assume the most varied forms corresponding to a subdivision of labour. Ultimately the uppermost and last-produced members of the plant are transformed into flowers and fruits. It is thought that, just as a plant is gradually differentiated in this way so have all plants undergone a similar transformation, step by step. The egg-cell, the starting-point of the individual, may be compared to a Myxomycete, the cell-complex which arises from the egg-cell after fertilization to a Thallophyte, the segmented axis and appendages of the seedling to a Vascular Cryptogam, and the complete plant-body, finally, to a Flowering Plant.

This comparison, like so many others which captivated the imaginative faculties in the days of the speculations of nature-philosophy, has found many adherents; indeed, it has served as dogma and guiding light in many investigations. But it is difficult to harmonize it with other theories well-proved by experience. The main burden of this comparison (known as the "Recapitulation-theory") is that the vegetable kingdom as a whole has undergone a developmental history and transformation resembling that of a single member of the group of Flowering Plants. But first it must be asked, what is the meaning of metamorphosis in the individual, and what object has been attained by it? Though the actual processes taking place in the living protoplasm in metamorphosis are unknown, this much seems certain: That these changes occur along lines sufficiently well indicated; that the fashioning of the successive stages of any given species is accomplished according to a definite plan; that external influences, such as soil and climate, do not permanently affect this plan; and that consequently the plan of construction of these successively appearing stages is laid down in the protoplasm itself. The ultimate object of metamorphosis in plants is the production of fruit; and with the formation of an ovary the metamorphosis ends, the fertilized egg-cell beginning the metamorphosis all over again, *i.e.* it is the starting-point of a series of transformations along identical lines. And this applies equally to the Apple-tree and to the Palm, to the Pine, the Horse-tail, the Moss, the Bladder-wrack, Stonewort, to the Mould, and to the simplest of green Algæ. Only in the last-named forms are the intermediate stages fewer than in the first-named. But it will hardly be suggested that the latter have not on this account attained the end in view. Simple plants whose fertilization and fruit-formation is accomplished under water, whether it be on inundated land, in the mud of a river, or at the bottom of a lake, attain this end without a complex metamorphosis of petals and stamens; whilst many

of the denizens of the ocean have no need of segmentation into stem and leaf. Indeed, such a metamorphosis for this purpose would be a disadvantage, anything but a progressive development. Similarly is it inconceivable, from all we know of the relations between external conditions and the form of an organism, that a Fern (for instance), unable to accomplish its fertilization in dew or rain-water, should in consequence depart from its usual habit and strike out a new line of metamorphosis. Thus we may conclude[1] that the development of the individual (Ontogeny) cannot be regarded as an epitome of the ancestral history or line of descent of that individual, and, further, that ontogeny gives no support to the assumption of a ramifying phylogenetic tree starting with simple forms and ending with complex much-differentiated ones.

The results of developmental investigations showing a marked similarity in the form of organs serving similar purposes in the most different groups of plants have been brought forward in support of the assumption that Flowering Plants have arisen from simple Cellular Plants by a series of progressive transformations. Though these organs are in some groups of more simple, in others of more complex structure, their similarity is unmistakable; it is upon this that the view is widely based that organisms exhibiting similar organs have been derived from one another. But this inference is inadmissible. The similarity in question finds a simpler explanation as the expression of the attainment of a common object. Thus fertilization consists in the coming together and uniting of two portions of protoplasm which have originated at a distance from one another; the similarity of ways and means in attaining this object are obvious. In one case water is employed as a means, in another the air. There is, truly, a difference in detail, but the general similarity remains. From this general similarity all we are justified in inferring is that the organisms in question all reproduce themselves by fertilization, not that they have a common origin.

This conclusion leads to the question whether, in view of the diversity of the organs of fertilization, several distinct stems of plants may not have co-existed all along. We know from observation and experiment that new forms do not as a rule arise from offshoots, but from fruits. New groups of plants might thus (so it was said) arise from existing ones solely by the sexual method. Complex Thallophytes might arise from the fruits of simpler ones, Ferns from the fruits of Mosses, and so on. Assumptions of this kind belong to a period at which the phenomena of fertilization and fruit-production, especially in the Cellular Plants, were only very imperfectly understood. No Botanist nowadays would suggest the possibility of a *Spirogyra* or a *Ulothrix*, or an *Œdogonium*, or a Stonewort, arising from the fruit of a *Vaucheria*. It might well happen that a new species could arise by the crossing of two dichogamous species of *Vaucheria*, but this new form would be essentially a *Vaucheria*, and its methods of fertilization would be essentially similar to that of its parent-forms. It is likewise as impossible for the male protoplasm of a *Vaucheria* to enter the chamber in which the conjugation of the

[1] See editorial note prefacing this volume.

sexual cells of *Spirogyra* takes place (*cf.* vol. i. Plate I. fig. l), or for this spermatoplasm to fuse with the gametes of *Ulothrix* (*cf.* p. 49), as for the gametes of *Ulothrix* to enter and fuse with the egg-cell of a *Vaucheria*; no new group of plants could have arisen in this way. We may conclude then that plants belonging to groups with a marked diversity in their sexual characters have not arisen from one another, but belong to stems which have co-existed as distinct types from the first.

Nor must we omit to notice the observations which have been made in regard to symbiosis and the inter-relations of green and non-green plants. It has already been pointed out (vol. i. pp. 263, 264) how that the continuation of plant-life, and indeed all life, is dependent on the activity which saprophytic plants exhibit in the decomposition of dead organisms. Green plants could not exist independent of colourless saprophytes, nor these latter without green plants. This must ever have been the case, and it must so remain. We may then draw another conclusion, viz. that those colourless plants which by their activity bring about the decomposition of green plants cannot have arisen from green plants, but that from the beginning they have belonged to a distinct stem.

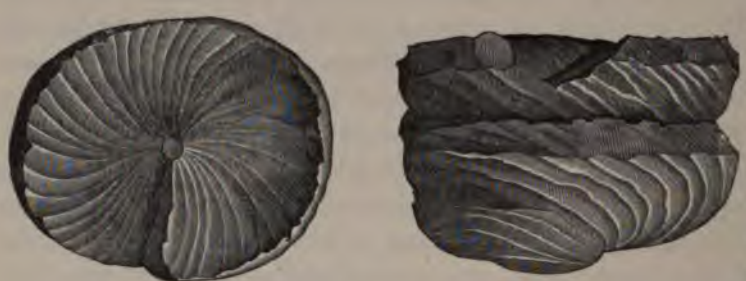


Fig. 305.—*Spirophyton* from the Upper Devonian.

It is to Palæontology that we must look for the most trustworthy solution of the question as to whether numerous plant-stems have existed side by side from the first, or whether the groups which at present co-exist have in process of time branched forth from a single stem. Were it a fact that those forms which show a far-reaching division of labour, and a complex structure of organs, which we term "higher plants", have arisen from others of very simple mode of life and possessing a simple structure and which are known as "lower plants", then should we expect the earth to have been covered formerly by lower plants alone. And then, following this epoch, would have come a time when plants would have existed which might have served as the starting-points of the later-appearing distinct groups. We should expect to find in those strata of the earth's crust regarded by geologists as the oldest of all nothing but the remains of very simple Thallophytes, then, following these, Wracks, Red Sea-weeds, and Lichens, and after these Stoneworts (*Chara*), Mosses, or some other type of plant which, having given rise respectively to Stoneworts and Mosses, has, after this differentiation, become extinct.

From the graphite, which is looked upon as the oldest trace of vegetable life on the earth, unfortunately we obtain no conclusive evidence on this matter. From its presence on slate mountains together with crystalline limestone and pyrites

we might conclude that it originated from plants adhering to the limestone reefs formed by animals or from sea-plants which lived on the borders of these limestone cliffs. Where graphite is found in greatest quantity one is tempted to think it might have been derived from peat moors. As we have said, all these are merely suppositions, for since the carbon, lime, and silicates have become crystalline all the points for the determination of the families to which the graphite-forming plants belonged are lacking. It might be noted here, by the way, that although graphite does indeed furnish the oldest traces of plant-life on the earth this does not prove that the plants which gave rise to it were necessarily the first which

Fig. 366.—*Riella helicophylla* growing under water. Enlarged.

existed there. It is doubtful whether the rock which is associated with graphite formed the first hard crust of the earth. Much more probably this rock was composed of other broken rocks just as it has itself been again demolished, furnishing the material for new strata.

The shapes of vegetable remains from palæozoic formations are fairly easily recognizable. Those which were formerly regarded as fossil Sea-wracks have indeed been more recently interpreted as the trails of worms and medusæ, but some of them are without doubt the remains of Sea-wracks. The only other known lowly plant which at that time had an aquatic habit is the curious *Spirophyton*, the so-called Cock's-tail Alga (see accompanying fig. 365). This, though some regard it as of purely inorganic origin, may perhaps be regarded as a submerged Liverwort; at any rate it is not without resemblance to *Riella Reuteri*, which at the present time lives in the Lake of Geneva, and to the Algerian *Riella helicophylla* (see fig. 366). No trace is to be found of Thallo-

phytes which may have existed on land, but we have huge tree-like Vascular Cryptogams with trunks, fronds, and leaves which are to be placed side by side with our present-day Equisetums, Ferns, and Lycopods. Cycads and Conifers also are not absent from the Coal Measures. No Angiospermous flowering plants have hitherto been demonstrated in these strata, but it would be foolish to regard this fact as a proof that neither Thallophytes nor Angiosperms flourished at this period. That which has been preserved to us from this time certainly forms but a small fraction of the old vegetation, and is restricted apparently to the flora of peat-moors which were just as poor in species and just as monotonous as they are to-day. The plants which at the present time predominate on the moors are still the Equisetums, Ferns, Lycopods, and Conifers, and, in tropical regions, the Cycads; only a few species from each group, but standing in thousands side by side and aggregated into dense communities. Anyone who has worked out the history of these moors knows that the soil must have been prepared for these plants by other growths. *Equisetum limosum*, *Aspidium Thelypteris*, *Lycopodium inundatum*, &c., do not flourish in soil poor in humus; in order to obtain their requisite food and to develop they require soil which is saturated with the dead remains of earlier settlers. Experience tells us that the plants which appear as the first inhabitants belong to widely different groups (see vol. i. p. 268). Now if we hold to the view that the formation of peat-moors in long-past ages occurred just as in the present day, we must assume that the colonies of Equisetums, Ferns, Lycopods, and Cycads were preceded by other plants which, as the first settlers, prepared the soil. We cannot indeed determine from the surviving remains to which groups these first settlers belonged; but, looking back on the history of our present peat-moors, it seems not improbable that among them were both Thallophytes and Angiospermous flowering plants.

The fact that the fossil remains of Equisetums, Lycopods, and Cycads, which spread so widely over the peat-moors of palæozoic times, have reached us in such good condition is explained by the presence of humus-acids, which are formed universally in the peat (see vol. i. p. 263). There are four conditions which render it possible for a plant to be preserved as a fossil: humus-acids form the first; the second is the resin which exudes from the pine-wood and forms amber; the third is mud and sand brought by floods; and the fourth the silicification and calcification of the cell-wall or the formation of a lime incrustation which is precipitated from calcareous water on to the various parts of the plant. It is certain that these four conditions have always been effective, but it is doubtful whether all the fossils formed in the fourth manner at all periods have remained. For many older strata have long been destroyed and used in the building up of younger layers, and many risings and sinkings of these strata have taken place. It would indeed be difficult to find a single place on the earth's surface which has not been repeatedly above and under the sea. Much that might lead us to definite conclusions at present lies inaccessible to us, covered with immense masses of water at the bottom of the sea, and the view has actually been suggested from studies made on the few accessible

and closely investigated spots on the earth's surface that the fossil remains found there are not more than a minute fragment of the vegetation of periods long elapsed.

With these remarks we might mention that it is not beyond the range of possibility that, in addition to the Vascular Cryptogams, Cycads, and Conifers growing on peat-moors, plants of other habitats, especially those of fresh and salt water, or perhaps of sand-dunes and river-banks, might be found in the strata of palæozoic times. But no one would doubt that among these would be Angiospermous Phanerogams, and this throws some light on plant remains which have come to us from the mesozoic period. For example, in the upper layers of the chalk we find, in addition to the plants of peat-moors, the inhabitants of a luxuriant forest-flora of Angiospermous flowering plants. There are Planes, Birches, Beeches, Oaks, Poplars, Willows, Fig and Laurel trees, Maples, Ivy and other Araliaceæ, Bread-fruit trees, Tulip-trees and Magnolias, Cherry-trees, and Leguminosæ of the division Cæsalpineæ, Palms, Rushes, and Grasses. If we do not believe in the theory that these Angiosperms were first created in the mesozoic period, and still less in the greater marvel that they have sprung from the Vascular Cryptogams, Cycads, and Conifers, we are forced to the conclusion that they too must have existed as far back as the palæozoic time. It is to be specially noted that not the slightest trace of intermediate or transitional forms which might connect the aforesaid Angiospermic Phanerogams with the Gymnosperms or with the Vascular Cryptogams has been found. One leaf is immediately recognized as belonging to a Tulip-tree, a second to Maple, a third to a Fig-tree, a fourth to a Palm, &c., but no plant has been discovered anywhere which would perhaps form a connecting link between the Palms or Figs and the Conifers or Vascular Cryptogams.

Even a cursory glance at the plant-forms named shows that they were members of mixed forests. It may be assumed, however, that other plant communities peopled the earth at the same time as these forests. The rocky terraces and boulders, as well as the flat dry land, were certainly not destitute of vegetation. Nor is it surprising that no fossil remains of the inhabitants of these places have remained. The under-shrubs and herbs of a dry soil decompose immediately after their death, and leave behind only formless humus, which mixes with the soil. Just as little fossil remains will reach posterity of the Lichens and Mosses, Pinks and Composites, Saxifrages and succulent plants which inhabit the rocks on the dry mountain-slopes at the present day, as of the Tulips and Irises, Umbelliferæ and Saltworts of the steppe-flora; and a great mistake would be made if, millions of years afterwards, it were reasoned from the lack of fossil remains of these plants that they could not have existed in our time. It would be just as wrong for us to argue from the absence of such plants in the strata of earlier periods that they had never existed in those times. The same thing applies to most fresh-water and marine Algæ, and to the numberless saprophytes which effect the destruction of dead animal and vegetable bodies above and under water, and thus maintain the eternal cycle of life as a whole. Of the first-mentioned the only fossil remains which can be recognized

are those of Diatoms, whose cell-wall is transformed into an imperishable siliceous frustule, together with those Florideæ which provide themselves like corals with a calcareous skeleton, and some tough Sea-wracks. It is, however, a very significant fact that the innumerable fossil Diatoms which come to us in so-called tripoli-powder and Diatom-earth, and the many calcareous Florideæ which come down to us as Nullipore banks are deceptively like those living at the present day, that these groups have remained unaltered for eons, and that no form has been discovered in any of the older strata which could be regarded as a link with another group. No fossil remains are known beyond doubt to exist of the numerous aquatic plants with delicate cell-walls which perish as rapidly as they develop, of the *Sphærella* species which give a red colour to rain-water and to the snow-field, of the microscopic Desmids, of the green filaments of *Spirogyra*, of the remarkable green tubes of *Vaucheria* pictured in fig. 25A, &c. Some woody *Polyporus* species of Fungi have reached us, but in forms which look very like those at present growing on old tree-trunks. Some species of Moulds have been preserved in amber. I have before me a piece of amber in which insects are imbedded; from one of them spreads a web of mycelial threads which doubtless belonged to some mould-like Fungus such as to-day attacks various insects. The myceliums of various Fungi, also, are found penetrating the tissues of many of the fossil cryptogamic stems of the Coal Measures. This fact is very instructive, since it shows that in the tertiary period, and in much earlier periods also, the relation of saprophytic plants to the dead bodies of animals and plants were the same as they are to-day. All these results taken together prove that delicate Thallophytes whose cells do not become siliceous or calcareous, or which are not inclosed in resin, cannot be preserved in a fossil condition. But no one would conclude from this that the groups to which such delicate growths belong were not represented in earlier periods.

On comparing the past and present of the Vegetable Kingdom from these points of view, more especially with regard to the question whether existing groups stood side by side in earlier periods also, or whether, in the course of time, they have sprung from a single individual or from a few spontaneously-generated individuals, we are obliged to decide in favour of the former. The so-called "higher" plants are not derived from the so-called "lower"; the groups of higher and lower plants co-existed from the beginning side by side. But variations within the limits of each group have always taken place. New species, *i.e.* new groups of species, arose in consequence of the crossing of the species already in existence. Of these the species which were best suited to the climatic conditions of the time being survived. But the variation in the formation of new species never went so far as to do away with the characteristics of the group. We immediately recognize in the fossil Laurel-trees, Magnolias, Oaks, Palms, Grasses, Pines, Equisetums, Ferns, Lycopods, Florideæ, Diatoms, and Moulds the ancestors of the now existing species. This would be impossible if the group-characteristics had disappeared in the modifications which the species have undergone.

When I now attempt the task of stating in detail what has been furnished by

theoretical considerations, and of bringing forward the various groups which have from the beginning existed side by side, distinguishing them by the enumeration of their peculiar characteristics, I am not blind to the enormous difficulties of the undertaking. Although Palæontology, Morphology, and Physiology afford valuable results, they are not enough, and neither of the three sciences gives sufficient data for the complete solution of the problem. One of the greatest obstacles is the aforesaid incompleteness of the geological record. From the existing remains we may indeed conclude on the whole that numerous groups stood side by side in the mesozoic and palæozoic periods, but the evidence of many groups which exist at the present day without transitional forms is wanting, and when we assume their existence we make use indeed of a justifiable hypothesis, but have no proof whatever. The danger, on the other hand, of establishing homologies from the similarity of an organ which is observed in groups of species now living has already been mentioned (see p. 609). Up to a certain point all organs which have similar work to perform agree with one another. This agreement is the more pronounced the greater the similarity of the conditions under which the organs have to do the work. Species of very different groups which live under water exhibit many characteristics in common; plants whose pollen-grains are transported by the wind show a great agreement in the structure and position of the parts of the flower. In the same way the form of flower-visiting insects necessitates a number of similar characteristics in the flowers visited. For example, we might instance the sweeping hairs on the style of the Proteaceæ and of the Composites, as well as certain developments which are met with in the flowers of Aroids, which are visited by small flies, and also in the Aristolochiaceæ. In spite of this consideration, however, the similarity in the structure and form of organs, both of those serving for propagation and for nourishment and growth, must obviously be kept to the forefront; similarity must always be an important factor in the limitation of groups.

As we have in the preceding chapter established the fact that each species is built up by protoplasm with a specific constitution, the question might be propounded whether each plant-group has not something in common in this respect. Many observations argue differently for this view. It has been repeatedly stated that the Moulds, Oscillatorieæ, Sea-wracks, Stoneworts, &c. give off a scent which, although it differs according to the species, is yet very similar upon the whole, and that one is justified in assuming a specific constitution of the protoplasm in each of these groups on this account. Moreover, the scent which the Mosses exhale is found in no other group of plants. The same is true of Ferns. The delicate fronds of the tropical Filmy Ferns exhale the same peculiar scent as the larger Ferns of our forests. The Coniferæ, Umbelliferæ, Labiateæ, Leguminosæ, and Cruciferæ exhibit similar conditions. Is it not also a striking phenomenon that the parasitic Fungus *Cronartium asclepiadeum* should settle on *Cynanchum Vincetoxicum*, as well as on *Gentiana asclepiadea*, *i.e.* upon two plants which the Botanist certainly places in different families, but which he regards as belonging to the same alliance? To these facts many others might be added, especially with regard to the choice of

vegetable food by animals. But our knowledge in this respect is so fragmentary and uncertain that for the present we cannot make use of these conditions in the limitations of the groups.

The capacity for sexual union is of the utmost importance in defining plant groups. Species which can unite sexually belong undoubtedly to the same group. Nothing can be urged against this principle, and if it could be universally applied, the division of the groups would be settled. But in this matter there are very many pros and cons. The converse of the proposition requires consideration. It will not do to say that all plants which cannot unite sexually belong to different groups. It has been shown that crossings can be successfully effected in Orchids which all Botanists regard as members of different genera, but, on the other hand, it is demonstrated that crossings between very similar species of the Umbellifer family lead to no fruit formation. No one, however, would conclude from this that these Umbellifers belonged to different groups. On reflecting in what a small number of flowering plants the fertilizing process has hitherto been observed, and remembering that the fertilization of many Thallophytes is still totally unknown, the hope of being able to utilize these conditions in limiting the groups becomes very much lessened.

In the review of the various groups of the vegetable kingdom which follows[1] no attempt is made to present the groups in the form of an ideal natural system. So far as the Thallophytes, Bryophytes, Pteridophytes, and Gymnosperms are concerned, there is a very general consensus of opinion amongst Botanists, and the serial arrangement here followed is in harmony with it. But as regards the Angiospermous flowering plants, and in particular the Dicotyledons, it is as yet too early in a book of this nature to embody all the most recent suggestions as to the affinities of the various families. Attention was drawn on p. 605 to the system of Alexander Braun, and it was pointed out that he was the first to try and break up the large and unsatisfactory class Monochlamydeæ or Apetalæ, and to relegate its families in part to their true position. This attempt has been very fully carried out by Eichler (1883), and by Engler (1892); these two Botanists admitting only two classes of Dicotyledons (Choripetalæ or Archichlamydeæ and Sympetalæ). But as yet many of their placings of individual families are but tentative, and we may well wait a few years for a system on these lines to settle down into more or less permanent form. An instance of too hasty rearrangement of a natural system to meet recently discovered facts may be quoted here. In 1891 Treub discovered that *Casuarina* possessed chalazogamic fertilization, and in 1892 Engler (following Treub) separated *Casuarina* from all other Angiosperms as the sole genus in a new class Chalazogamæ. Since then it has been found (see p. 413) that chalazogamic fertilization is much more general than was at first supposed, and that in the group Amentaceæ it is widely spread though by no means of universal occurrence. To break up the Amentaceæ in the drastic manner involved, if the class Chalazogamæ be maintained, seems a mo

[1] Cf. editorial note at commencement of this volume.

undesirable and unnatural thing to do; it will on the whole be best to abolish a special class of Chalazogams, and, if thought necessary, to rearrange the families which constitute the Amentaceæ, but not to sever them from one another. For the Angiosperms we shall in the main follow the arrangement of the well-known *Genera Plantarum* of Bentham and Hooker, though we reserve our freedom to deal with certain families as seems well to us.

The vegetable kingdom we divide first into four main divisions or *phyla:* (1) The Myxothallophyta, including the Myxomycetes only, a group standing apart from (2) the Thallophyta, which include the various classes of Algæ and Fungi. Then follows (3) the Archegoniatæ, forms possessing archegonia and fertilized by motile spermatozoids, and including the Liverworts and Mosses, and the series of the Ferns (Phyla (1) (2) and (3) constitute what are usually referred to as "Cryptogams"), and (4) the Phanerogamia or flowering plants, fertilized by means of pollen-tubes. They fall into two sub-phyla, Gymnosperms and Angiosperms, and the latter into two classes, Monocotyledons and Dicotyledons. Finally we have the 3 sub-classes of Dicotyledons—Monochlamydeæ, Monopetalæ, and Polypetalæ. Here, in outline, is the system:—

(1) MYXOTHALLOPHYTA, containing 1 class only.

(2) THALLOPHYTA, containing 5 classes.
- I. *Schizophyta.*
- II. *Dinoflagellata.*
- III. *Bacillariales.*
- IV. *Gamophyceæ.*
- V. *Fungi.*

(3) ARCHIGONIATÆ, containing 2 classes.
- I. *Bryophyta.*
- II. *Pteridophyta.*

(4) PHANEROGAMÆ, containing 2 sub-phyla.
- A. GYMNOSPERMÆ.
- B. ANGIOSPERMÆ, containing 2 classes.
  - I. *Monocotyledones.*
  - II. *Dicotyledones*, containing 3 sub-classes.
    - *a.* Monochlamydeæ.
    - *b.* Monopetalæ.
    - *c.* Polypetalæ.

Each class (or sub-class) is further divided into a number of cohorts or *alliances*, and each of these alliances into orders or *families*. The alliances will be taken one by one in the following pages, their main characters generally indicated, and the families which they comprise enumerated. It will not be possible within the limits of this book to deal with the several families in at all a comprehensive manner, though the endeavour will be made to point out structural and other characters of interest, and where certain genera or groups of genera have a special interest these will be alluded to. No attempt is made to observe any due sense of proportion in treating of the different alliances. Thus a small alliance containing but few members of especial interest will receive more detailed consideration than one vastly

larger, the numerous representatives of which are unrelieved in their monotony. This method, truly, is an unconventional one, but in view of the restrictions of space, perhaps better suited to our purpose than any other.

PHYLUM 1.—MYXOTHALLOPHYTA.

Organisms destitute of chlorophyll, whose vegetative state consists of a mass of naked protoplasm (plasmodium). Reproduction by spores, from which arise swarm-spores or myxamœbæ, which unite again into plasmodia.

Alliance I.—Myxomycetes, Slime-Fungi.

For the most part saprophytic upon dead organic and especially vegetable substances; they occur chiefly on accumulations of the dead parts of plants—leaves,

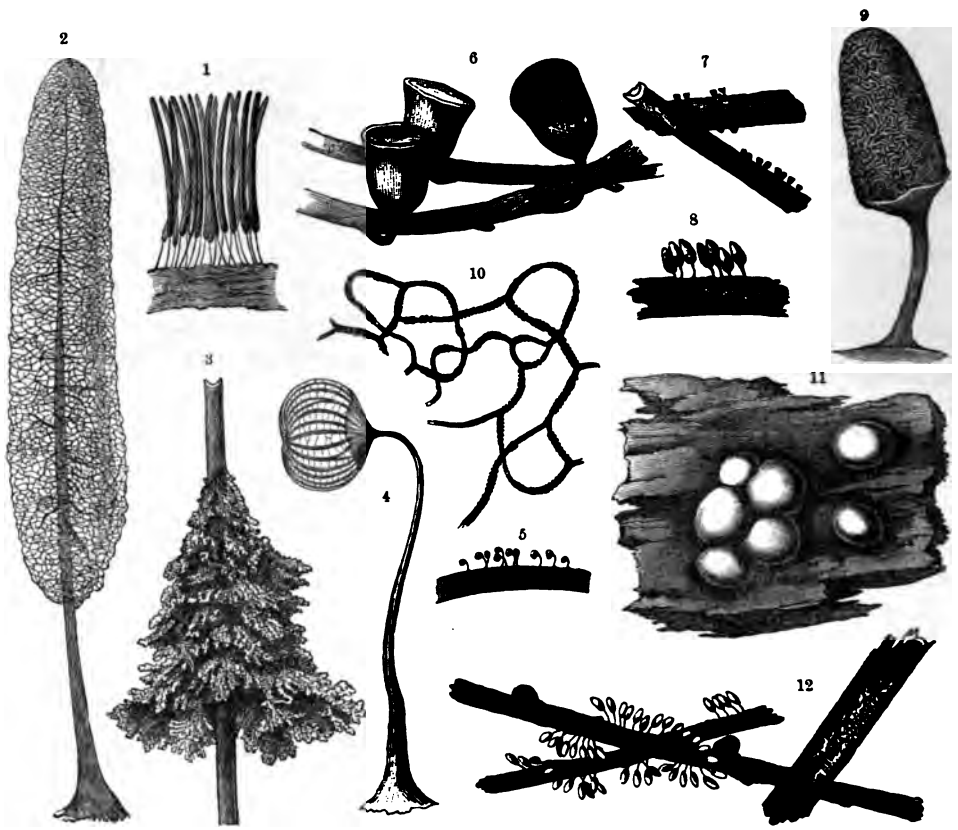


Fig. 367.—Myxomycetes.

[1] A group of sporangia of *Stemonitis fusca*. [2] A single sporangium; × 6. [3] Dendritic mass of sporangia of *Spumaria alba* on a Grass leaf. [4] Sporangium of *Dictydium cernuum*; × 25. [5] A group of sporangia of the same. [6] and [7] Sporangia of *Craterium minutum*; [6] × 25. [8] Sporangia of *Arcyria punicea*. [9] A single sporangium; × 10. [10] Part of the net-like capillitium of the same; ×160. [11] Fructification of *Lycogala epidendrum* on a piece of wood. [12] *Leocarpus fragilis*; a plasmodium on the right; several sporangia on the left.

tan, rotting wood, and the like; they are rarely parasitic. Their life-history is as follows:—On the germination of the spores the membrane bursts, and a slimy, nucleated mass of protoplasm escapes, which either swims in water by means of a

single flagellum, or creeps about on a damp substratum; these motile bodies are the *myxamœbæ*. These amœbæ increase at the expense of absorbed nutriment, and undergo repeated division. Ultimately they fuse together into masses of naked protoplasm—the *plasmodium-stage*—which creep about until spore-formation sets in. The plasmodium is transformed into the reproductive stage, numerous sporangia arising all over its surface. This stage in different cases shows the most varied structure, as may be seen by reference to fig. 367. Either the whole plasmodium is transformed into a single sporangium, as in *Lycogala epidendrum* (fig. 367 [11]), or a number of sporangia arise. A portion of the protoplasm becomes hardened to form the wall of the sporangium, whilst the contents is resolved into a mass of dust-like spores. In addition there arises in the majority of forms a sort of internal skeleton, the *capillitium*, which may consist either of a number of elongated tubes with characteristic thickenings on their walls, or these tubes may be united together into a continuous network (fig. 367 [2]). On the bursting of the sporangium the spores are scattered and carried away by currents of air. They germinate when they reach a moist substratum, and the life-cycle is passed through anew. Under unfavourable conditions a plasmodium may become encysted, forming a transitory resting-stage. If placed in water, the plasmodium escapes from the cyst, and continues its life-history even after a lapse of several months. The substance of the membrane, whether of the sporangial wall, spores, or capillitium, does not seem to consist of cellulose, but rather of a congealed protoplasm. We see, then, that the life-history of a Myxomycete is divided into a nutritive stage consisting of naked, membraneless, protoplasmic masses, and a sporangial, spore-producing stage. In respect of their nutritive stage the Myxomycetes very nearly resemble certain groups of the Protozoa, and on the strength of this resemblance they are regarded by many Botanists and Zoologists as belonging rather to the animal than to the vegetable kingdom. In their manner of reproduction they certainly show analogies to many of the Fungi however.

Plasmodiophora Brassicæ is a parasitic Myxomycete which attacks the roots of the Cabbage, causing the disease known as "Fingers and toes" (*cf.* p. 522).

Fossil Myxomycetes are not known. About 450 species have been distinguished.

Phylum 2.—THALLOPHYTA.

A large and very heterogeneous collection of plant-forms is included under this term. The word (Greek θαλλός, and φυτόν) literally means plants with undifferentiated *shoots*, and includes practically all plants standing below the Mosses and Liverworts in complexity of organization. It is impossible to characterize positively a group, or rather a collection of groups, which shows so wide a range of organization as we find among the Thallophytes. They are often characterized negatively as plants whose bodies show no distinction between axis and appendages (stem and leaves). To such a plant-body the name *thallus* is given. But though this definition holds good for the great majority of the Thallophytes, yet there are forms (e.g. *Bryopsis*,

the verticillate Siphoneæ, *Draparnaldia*, many of the Brown Sea-weeds) which do show a distinction between axis and appendages, though the distinction is not usually so marked as that between the stem and leaves of a higher plant. Similarly, though for the most part possessing a relatively low organization, some Thallophytes (especially the higher Fungi and certain of the Brown Sea-weeds) show considerable differentiation of structure. The *Thallophyta* consist of many divergent and more or less sharply characterized groups. These include the Green Algæ (*Chlorophyceæ*, which includes the alliances Protococcoideæ, Siphoneæ, Confervoideæ, Conjugatæ, and Charales), the Brown Sea-weeds (*Phæophyceæ*), the Red Sea-weeds (*Rhodophyceæ* or *Florideæ*), the Blue-green Algæ (*Cyanophyceæ* or *Schizophyceæ*), the Bacteria (*Schizomycetes*, here included with the last-named group in one class, the *Schizophyta*), the Diatoms (*Bacillariales*), and the Fungi. Some Botanists consider that the Myxomycetes (or *Mycetozoa*), and the Dinoflagellata (*Peridineæ*) are also plants. These last groups are almost certainly branches of the Protozoa; and though possessing certain plant-like characters (as indicated above), they show no near affinity with other plant groups. Whether they should be considered as plants or animals must therefore remain a matter of opinion.

The same may be said of certain other organisms regarded by zoologists as Flagellate Protozoa, but showing undoubted affinities with the lower forms of Green Algæ. There exists, in fact, an unbroken series of forms, connecting undoubted Protozoa, having mouths by which they eat solid food, with undoubted green plants depending entirely on soluble inorganic food. The dividing line between animals and plants is here obviously an artificial one, and is naturally drawn by different authorities at different points in the series.

The name Thallophyta, then, is given to all plant-forms below a certain grade of organization, and includes many separate and widely divergent lines of descent. The Thallophytes may be pictured as the shrubby growth around the base of the phylogenetic tree representing the plant kingdom. The lower part of the main trunk of the tree, that is to say, the line of descent by which the higher plants have originated, is probably represented by certain of the Green Algæ.

Class I.—SCHIZOPHYTA.

For the most part exceedingly small organisms, which propagate entirely by asexual methods. They consist of isolated cells, cell-filaments, surfaces, or masses. Though till recently regarded as without nuclei, these bodies have been found in a number of forms, and this view is being abandoned. They include both coloured and colourless forms; but the coloured forms never exhibit pure chlorophyll.

Alliance II.—Cyanophyceæ, the Blue-green Algæ.

Families: *Chroococcaceæ*, *Nostocaceæ*.

Includes pigmented forms in which in addition to chlorophyll *phycocyanin* is present, giving the cells a bluish, violet, or reddish tint. They occur in water or in moist places, and their cells may be united together into aggregates of various kinds. The cell-walls are usually mucilaginous, so that the cells or filaments cling together in colonies, or they are inclosed in special sheaths. The simpler forms included under the Chroococcaceæ are unicellular; the products of their division may either remain united into colonies or become quite free from one another. The rest are filamentous, and are included under the Nostocaceæ, whose filaments can become segmented into small portions which move away by a peculiar motion not yet fully understood (*cf.* vol. i. p. 40). At times also certain cells become resting-spores and can endure climatic vicissitudes. They are widely dispersed over the globe, and are met with in cold glacier-streams and have been found living in hot springs at a temperature of even 85° C. Some 800 living species are distinguished.

Chroococcaceæ.—Includes the unicellular forms. *Glœocapsa* (vol. i., fig. 25 A, *n*, *o*) forms little mucilaginous colonies, often found on the moist window-panes of hot-houses. *Merismopedia* forms films on stagnant water, and *Clathrocystis* like certain of the Nostocaceæ (alluded to below) arises in quantity in water. A form probably referable to this group (*Dermoglœa Limi*) developed in 1874 in such quantities off the Adriatic coasts as to seriously interfere with the fishing industry. A commission was appointed to investigate the matter, but in six weeks the *Dermoglœa* vanished as suddenly as it had appeared.

Nostocaceæ are, for the most part, filamentous, though in some forms the cells may become isolated. *Nostoc* itself is common, and takes the form of irregular gelatinous colonies, which contain numerous interwoven necklace-like filaments. In some districts, owing to its sudden appearance after rain, it has received the name of "Falling Stars". This explains the allusion in the following lines from Dryden's *Œdipus*:—

> "The tapers of the gods,
> The sun and moon, run down like waxen globes;
> The shooting stars end all in *purple jellies*,
> And chaos is at hand".

A species common in China, *N. edule*, is used as a thickening for soup, and an allied form, *Hormosiphon arcticus*, abounds in the Arctic regions upon floating ice. *Anabœna Flos-aquæ*, *Aphanizomenon Flos-aquæ*, &c., appear in fresh and brackish water—sometimes in enormous quantities, and to considerable depths. The *Trichodesmium Erythræum*—another of these "flowers of the sea"—referred to at vol. i. p. 389, belongs also to this group. Very little is really known about the life-histories of these interesting plants, which so frequently appear in great quantities at or near the surface of the water and then as mysteriously disappear. But now

that systematic observations are being made of the organisms which occur at the surface (*e.g.* at the Biological station on the Plöner See, Schleswig-Holstein) we may hope that these lacunæ in our knowledge may be filled up. Recent investigations (by Klebahn) upon several of these "flowers of the sea" (*Gloiotrichia echinulata*, *Anabœna Flos-aquæ*, *Aphanizomenon Flos-aquæ*, *Trichodesmium*, &c.) seem to indicate that they possess special organs of flotation designated "gas-vacuoles". It would appear that these natant forms have in consequence a smaller specific gravity than the surrounding water, and if the surface be quite unruffled tend to float, whilst any disturbance, such as waves, &c., is sufficient to cause their distribution through the upper layers of the water. Whether these "flowers" pass another stage deep down in the water is not fully ascertained. Their spores, so far as they have been observed, do not seem to possess "gas-vacuoles", and sink to the bottom. The phenomenon here indicated is not unlike that occurring in the Protozoon *Arcella*, the protoplasm of which is able by secreting a bubble of gas to rise to the surface, and, by absorbing it, to cause the organism to sink. The *Oscillarias* consist of filaments of disc-like cells; they exhibit curious gliding movements, which have been already alluded to (*cf.* vol. i. p. 40). *Rivularia* is distinguished by the fact that its filaments are whip-like, ending in a fine point, whilst in *Scytonema* this distinction of base and apex is not found. They generally occur in more or less mucilaginous masses.

A number of the Schizophyceæ are associated with certain Fungi to form Lichens (*cf.* later, and vol. i. p. 244); and certain of them occur embedded in the tissues of other plants. Thus species of *Nostoc* are met with in certain Liverworts (*Anthoceros*) and in the roots of *Cycas*; and *Anabœna* in special cavities in the leaves of the Rhizocarp *Azolla*. It is not known what may be the exact physiological relations between these Blue-green Algæ and the plants they inhabit—whether they are parasitic or symbiotic.

Alliance III.—Schizomycetes, the Bacteria.

On the whole, in the matter of their structure and aggregation, present many characters in common with the Blue-green Algæ. They are, however, destitute of the characteristic pigment of that group, and pass their lives as parasites and saprophytes, obtaining their food from ready-formed organic matter. Nuclei have been distinguished in some few forms, and the cells are inclosed in a membrane which, though often mucilaginous, does not consist of cellulose. In size the cells reach very small dimensions, and may be regarded as the smallest of all plant-forms. A number of different forms are distinguished; the Cocci, consisting of minute round cells; short rod-like forms, the Bacteria; longer rod-like forms, the Bacilli; various spiral forms known as Spirillum, Vibrio, and Spirochæte; filamentous forms, Leptothrix and Crenothrix. A very common mode of occurrence of the various forms is in gelatinous masses, to which the name Zoogloœa has been applied (*cf.* fig. 368[2]). Propagation takes place vegetatively by cell-division so long as the

conditions remain favourable for further growth. When the substratum is exhausted, &c., spores are formed which can remain for long periods—until, indeed, circumstances are again favourable for renewed development. These spores may arise either inside the bacterial cells (=endospores), the protoplasm contracting somewhat and forming a new wall around itself, or the cells may become transformed entirely into spores (=arthospores), the wall becoming specially thickened. In no case is there any sexual process. Whilst many Bacteria are only known under certain forms and are regarded as species of the genera *Micrococcus*, *Bacterium*, *Bacillus*, *Spirillum*, &c., others are known which, in the course of their development, pass through several such forms, and are termed pleomorphic. That all Bacteria are thus pleomorphic seems improbable, though the discovery that pleomorphism existed at one time led to the wildest generalizations. Large numbers of Bacteria display an active movement which, though formerly attributed to various contractions of their bodies, are now known to be due to cilia. These cilia may be borne in tufts of 5 or 6 at the two ends of the organism, as in *Spirillum Undula*, or they may be solitary at one extremity, as in the Cholera Bacterium (*Spirochæte choleræ asiaticæ*), or they may be scattered over the surface of the organism, as in the Hay-bacillus, *Bacillus subtilis*. It is due to the extreme fineness of these cilia that they were not recognized long ago.

Though the forms under which Bacteria occur are relatively few, their mode of life and special activity is exceedingly varied. The interest attaching to Bacteria rests largely on their effects on the substratum from which they draw their food. Taking, first, the saprophytes. These split up their substratum into simple substances. In some cases there is a complete oxidation, with production of carbon dioxide and water; in others this is only partial, as in some of the cases of fermentation, *e.g.* when alcohol is oxidized into acetic acid by the activity of the vinegar organisms *Bacillus* and *Micrococcus aceti* (*cf.* figs. 368[3] and 368[4]). Or there may be a decomposition unaccompanied by simple oxidation, as in many cases of fermentation, *e.g.* as when sugar is split into alcohol and carbon dioxide. Often these operations are accompanied by the development of a foul-smelling gas, when we speak of putrefaction. The number of saprophytic Bacteria which excite characteristic splittings in their substrata is considerable. In addition to those already quoted, we may mention *Bacillus Amylobacter*, the organism of butyric acid fermentation; *Bacillus lacticus*, which causes milk to become sour; *Leuconostoc mesenterioides*, which has the power of converting large quantities of sugar into a gelatinous mass in a very short space of time. Again, in a number of forms the production of a special colouring matter is associated with the activity of the organisms, as is the case with *Micrococcus prodigiosus* (*cf.* fig. 368[1]), the "blood-portent" which makes its appearance on various starchy food-stuffs, and *Beggiatoa roseo-persicina*, found on decaying vegetable matter in water, and known as "peach-mud". Many Bacteria are parasitic in the bodies of animals, and some among them are harmless. This is the case with *Sarcina ventriculi* (fig. 368[10]), known only in the human alimentary canal in the form of packets of cells. Harm-

less also are a number of Bacteria found on the mucous membrane of the mouth. On the other hand, many are associated with definite diseases. *Spirochæte Obermeieri* (fig. 368[9]) is found in the blood in great quantities during relapsing fever; *Bacillus anthracis* (figs. 368[7] and 368[8]) causes anthrax in cattle, &c.; and a great many other diseases—diphtheria, cholera (figs. 368[5] and 368[6]), tuberculosis, leprosy, &c.—are associated with the activity of specific bacterial organisms. Nor must we omit to mention the numerous forms which occur in the soil, some of which are concerned in the process of nitrification, *i.e.* which oxidize ammonia into nitric acid, thus rendering this source of nitrogen available to higher plants, whilst others

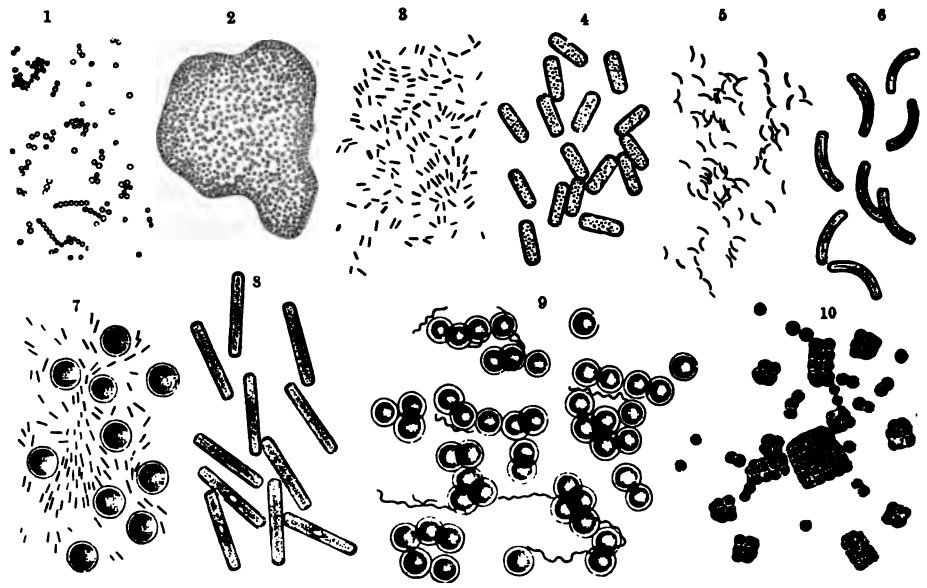


Fig. 368.—Bacteria.

[1] The "blood-portent," *Micrococcus prodigiosus*. [2] Zoogloea-form of same. [3] *Bacterium aceti*. [4] The same more highly magnified. [5] *Spirochæte choleræ asiaticæ*. [6] The same more highly magnified. [7] *Bacillus anthracis* and red blood-corpuscles. [8] The same more highly magnified. [9] *Spirochæte Obermeieri* and red blood-corpuscles. [10] *Sarcina ventriculi*. 1, 2, 3, 5, 7, 9 × 300; 10 × 300; 4, 6, 8 ×2000.

actually fix free nitrogen, as is the case with the organism occurring in the root-tubercles of many leguminous plants (*cf.* p. 521). There is no doubt this organism (*Rhizobium*, as it has been called) can store up free nitrogen, and that leguminous plants, when associated with it, obtain nitrogen not to be accounted for as combined nitrogen obtained from the soil. Curious also is the activity of the sulphur and iron Bacteria. The former (*e.g. Beggiatoa alba*) have the power of reducing the sulphates contained in the waters which they inhabit and of storing up sulphur-grains in their protoplasm; whilst the latter (e.g. *Crenothrix Kühniana*), not uncommon in water-pipes, where they often develop in enormous quantities, store up iron in the gelatinous sheaths of their filaments.

That Bacteria existed in former times, and were then, as now, the agents of decomposition, seems probable in view of the condition revealed by residues of dead

plants in the coal measures. It is thought that *Bacillus Amylobacter* has been identified in a silicified state.

Of living Bacteria a very large number have been distinguished.

Class II.—DINOFLAGELLATA, Peridineæ.

Alliance IV.

This compact group of unicellular organisms is, as has been said above, a branch of the Flagellate Protozoa. They have therefore no very near affinities with other plant groups, though the nutrition of many is thoroughly plant-like. They would come nearest to the motile (Flagellate) forms of Protococcoideæ (see p. 628).

The great characteristic of the group is the possession of two flagella, one directed longitudinally and attached to the anterior end of the body, the other transversely directed and often situated in a circular transverse groove. There is sometimes also a longitudinal furrow. It is this transverse flagellum which is specially concerned in movement.

There is often a cell membrane of cellulose, and the cell possesses green or brownish chromatophores containing chlorophyll and a single large nucleus.

Reproduction is effected by binary fission, usually during a resting stage of the cell.

Most of the forms are marine, and some are the cause of sea-phosphorescence.

The group is divided into two sections—the *Adinida* without, and the *Dinifera* with a transverse furrow.

Ceratium and *Peridinium* are two well-known genera.

Class III.—BACILLARIALES.

Alliance V.

Family: *Diatomaceæ*, Diatoms.

These are a large group of unicellular plants which grow both in fresh and salt water and upon moist soil. As a rule they occur together in large numbers. The protoplasm is coloured brown by a brown pigment, *diatomin*, which masks the chlorophyll which is also present. The colouring matter is restricted to special chromatophores, which may be few or numerous. The cell-wall is incrusted with silica, and is a very characteristic feature of the Diatom. The wall consists of two halves or valves (*frustules*) which fit into one another like the lid on to a pill-box. These valves are smooth or variously sculptured, dotted, ribbed, &c., and enjoy a wide popularity as microscopic objects on account of the beauty and delicacy of their tracery. Some idea of the variety and form of Diatom-cells may be obtained from the accompanying figure 369. In the colonial forms the cells are attached to the substratum directly (fig. 369 [1]) or by means of branching filaments (fig. 369 [14]). Others are attached to one another in zigzag chains or continuous ribbons (figs. 369 [15] and 369 [16]). Others, again, are embedded in mucilage. Many of the forms

exhibit a curious creeping movement, which is explained as being due to an external sheath or to filaments of protoplasm; the median line (or "raphe") shown by certain forms (e.g. *Navicula*, fig. 369 [4]) is interpreted as a narrow slit at which this external protoplasm is extruded. Diatoms propagate by continuous longitudinal division; the valves are slightly separated, and division takes place parallel to the faces of the valves. Each daughter-cell thus possesses one of the valves of the mother-cell, and they complete their integument by secreting another on the side away from it. The new valve is always slightly smaller than the other one and

Fig. 369.—Diatoms.

[1] Several individuals of *Synedra Ulna* attached to a cell of an aquatic plant. [2] A single individual of *Synedra Ulna* more highly magnified. [3] and [4] *Navicula Liber*, seen from the side and from in front. [5] and [6] Similar views of *Navicula tumida*. [7] *Triceratium Favus*. [8] *Campylodiscus spiralis*. [9] *Pleurosigma angulatum*. [10] and [11] *Grammatophora serpentina*. [12] and [13] Two views of *Gomphonema capitatum*. [14] *Gomphonema capitatum* on branched stalks which are attached to some algal filament. [15] *Diatoma vulgare*; the cells hang together into a zigzag band. [16] and [17] *Fragillaria virescens*, showing an individual from two aspects and a row of six joined together into a ribbon. [18] *Cocconema Cistula*. [19] Two individuals of *Cocconema Cistula* inclosed in a mucilaginous envelope preliminary to auxospore-formation. [20] The two auxospores have elongated, and the old cases are seen to right and left; there is no conjugation in this instance. All highly magnified.

fits under its rim, so that the Diatoms arising in this way become smaller and smaller till a certain minimum is reached. When this diminution has gone on for a certain period an enlargement is attained by the formation of what are termed *auxospores*. The contents of the cell gather themselves together, they become free from the valves, enlarge, and then put on new valves. In other cases an actual conjugation takes place, two individuals uniting into an auxospore; or each may divide into two daughter-cells, which fuse in pairs, forming two auxospores. Fig. 369 [19] shows two cells of *Cocconema Cistula* embedded in mucilage previous to auxospore-formation; in fig. 369 [20] each cell has escaped from its valves, and has doubled its original length. In this instance, however, there is no accompanying conjugation.

Diatoms are very widely distributed over the globe, and occur in quantities in

the surface layers of the sea; some 30 species have been found amongst the inorganic dust of the snow-field. There are some 2000 species of living forms.

Considerable deposits of Diatoms occur in various parts of the world; of these the most remarkable is that of Richmond, Virginia, U.S.A. It is said to extend for many miles and to be 40 ft. deep. They are found in secondary, tertiary, and more recent rocks. Siliceous marl consists entirely of the tests of Diatoms. A block of such a Diatom-deposit some two cubic feet in bulk from a fresh-water lake in Australia is exhibited in the Botanical Department of the British Museum; the number of Diatoms contained in it (there are 21 different species) is estimated as exceeding 12 billions (12×10^{12}).

Class IV.—GAMOPHYCEÆ.

Sub-class I.—Chlorophyceæ, the Green Algæ.

There can hardly be a more fascinating group of plants than this, whether to the strictly scientific botanist or to the more catholic lover of nature. In the first place, the Green Algæ are among the most widely diffused of plant-forms. They grow practically in every place where enough moisture, together with light and air, are to be had. Between tide-marks on almost every coast, floating on the surface of the deep sea, covering damp earth, walls, palings, and tree trunks, sticking to the surface of leaves in the moist atmosphere of tropical forests and jungles, and inhabiting almost every river, brook, pond, ditch, or casual pool of rain-water in all quarters of the globe, are members of this ubiquitous group to be found. Nor are they wanting from more extraordinary situations. In Switzerland, Norway, and other countries where snow is more or less permanent, the bright red patches on its surface, known as "red snow", are formed by the microscopic Alga (*Sphærella nivalis*) shown in fig. 25A, of the first volume. Other forms, not so far removed from *Sphærella*, live in the intercellular spaces of higher plants, such as the Ivy-leaved Duckweed (*Lemna trisulca*), the Moneywort (*Lysimachia nummularia*), and others. Yet other Algæ are found inhabiting the jelly of certain fresh-water sponges in the East Indies, where they seem to live in a regular symbiosis with their hosts. But perhaps the most curious dwelling-places of all are the hollow hairs of the Three-toed Sloth (*Bradypus tridactylus*), which are inhabited by an Alga called *Trichophilus*.

In the second place, many of the Green Algæ (and among these some of the very commonest) are the most beautiful forms of life imaginable, and the main features of their structure can be made out with quite low powers of the microscope.

But perhaps the greatest claim on our interest is made by the fact that we must look among the Green Algæ not only for indications of the origin of all plant life, and of the forms from which the whole of the higher plant world arose, but also for hints towards the solution of some of the most difficult and fundamental problems with which Biologists are occupied, questions as to the real nature and origin of sexual reproduction, as to the distinction between gametes and asexual reproduc-

tive cells, as to the physiological conditions which determine their formation, and finally, questions as to the division of labour in the protoplast itself, the function of the nucleus and its relation to the protoplasm, and how far the latter can be resolved into separate, but mutually co-operative parts.

The framework of our knowledge on the former group of questions has been, and is being, built up largely from a study of the Green Algæ; of the latter—and even more fundamental—we know, as yet, very little, but the same group of plants is already beginning to yield important results, and we have every reason to expect an even richer harvest in the immediate future.

We shall now proceed to a brief review of the groups into which the Chlorophyceæ may be divided, mention being made of the more interesting forms in each group.

The sub-class Chlorophyceæ may be defined as follows:—Thallus of very various form, one- or many-celled, coloured green by chlorophyll which is contained in chromatophores of very various shape: the green colour rarely masked by other pigments. Reproduction by motile *zoospores*, and by *gametes*, which either resemble small zoospores, and are equal in size (*isoplanogametes*), or are differentiated into two categories; first, relatively small, active male gametes—called *spermatozoids* when they are very highly differentiated—and secondly, relatively large, passive female gametes—known as *eggs* or *oospheres* when they are quite passive. The cell produced by the fusion of the bodies of two gametes is called the *zygote*, and gives rise to a new plant either mediately or immediately. When the gametes are sexually differentiated, the zygote (now called a *fertilized egg* or *oospore*) is produced only by the fusion of a male with a female gamete.

Other reproductive cells are known as *aplanospores* and *akinetes*. *Aplanospores* are formed by the protoplasm of a cell of the thallus rounding itself off and putting on a *new cell-wall*, or dividing into several parts, each of which acquires a separate cell-wall. *Akinetes* are simply single cells of the thallus, whose *original walls* thicken directly, the cells becoming separated from the rest of the thallus. These two categories of reproductive cells germinate at once to form new plants. The Chlorophyceæ comprehend the following alliances:—Protococcoideæ, Siphoneæ, Confervoideæ, Conjugatæ, and Charales.

Alliance VI.—Protococcoideæ.

Families: *Chlamydomonadeæ*, *Volvoceæ*, *Pleurococcaceæ*, *Endosphæraceæ*, *Hydrodictyaceæ*.

Unicellular forms, actively swimming, floating, or fixed in habit, living either singly or united into colonies.

Family *Chlamydomonadeæ*. This family consists of minute green (sometimes red) organisms which spend the greater part of their life actively swimming about in water. Several species of the genus *Chlamydomonas* are very common in stagnant water. Each *Chlamydomonas*-cell consists of a roundish mass of proto-

plasm covered by a delicate cell-wall of cellulose. At first sight the whole body appears green, but on careful examination it will be seen that the green colouring-matter is really confined to a layer on the surface of the body. This chlorophyll-layer or *chromatophore* is specially thickened at one end (the posterior end) of the body, and a small, clear, spherical body (the *pyrenoid*) is often to be seen inclosed in this thickened portion. Round the sides of the body the chromatophore is thinner, and towards the anterior end it stops, leaving a small area of colourless protoplasm to occupy the front extremity of the organism. This is in connection with another small mass of colourless protoplasm which occupies the hollow of the cup-shaped chromatophore.

A minute red speck is visible at one side of the body, situated sometimes on the surface, sometimes at the limit between the chromatophore and the central colourless protoplasm. The rotation of the *Chlamydomonas* about its antero-posterior axis, which accompanies the jerky, forward movement (*cf.* vol. i. p. 29) can be well traced by the aid of this eye-spot, which can be seen to be carried round and round as the organism turns on its axis. The means by which the *Chlamydomonas* moves are not at first sight apparent. But when the cell has come to rest, and especially if it has been killed and its protoplasm fixed with a dilute solution of iodine, a pair of very delicate protoplasmic filaments, called *flagella*, can often be seen projecting from the colourless anterior spot of protoplasm. It is by the continual lashing of these flagella that the *Chlamydomonas* is pulled through the water. The iodine will also bring into view a small spherical *nucleus*, stained dark brown, situated in the colourless central protoplasm, and will stain the neighbourhood of the pyrenoid a dark blue. This last phenomenon is due to the formation of starch by the protoplasm round the pyrenoid. The exact part played by the pyrenoid is very obscure, but there can be no doubt that it influences in some way the formation or deposition of starch by the protoplasm.

The movements of *Chlamydomonas* are often in direct relation to light, the organisms moving towards a source of light of moderate intensity. Thus if a glass vessel filled with water containing *Chlamydomonas* be placed in a sunny window, there will be a general movement of the swarming cells to the sunny side of the vessel, causing the water to become much greener on that side. There is some evidence that it is the eye-spot which enables the organism to perceive the direction from which light is proceeding. Nearly all the motile Protococcoideæ, as well as zoospores and gametes which are sensitive to light, possess an eye-spot, and it has been thought that the eye-spot-pigment (a substance called *hæmatochrome*) may act in the same way as the visual purple in the retina of the eye.

If specimens of *Chlamydomonas* be kept for a day or two in water, some of them will often be found to have divided to form daughter individuals, which still remain inclosed within the cellulose membrane of the mother. This division is preceded by the drawing in of the flagella. The protoplasm of the body then withdraws itself from the wall, and divides transversely to form two roundish masses. Each of the latter may either at once put on a cell-wall and develop flagella, or it may divide

again, so that four daughter individuals instead of two are formed. Eventually the daughters escape from the membrane of the mother, leaving it quite empty.

The process of reproduction by simple division of all the protoplasm of an individual's body into parts, each of which forms the body of a daughter individual, is an example of almost the simplest type of reproduction known. It is true that in the lower Protozoa, which have no rigid cellulose membrane, we find an even simpler type. Since the entire organism consists of protoplasm, there is nothing left of the parent individual after division has taken place. The body of the parent simply *becomes* the body of the offspring. In the type of *Chlamydomonas* we have the dead cellulose membrane representing all that is left of the body of the parent. In many of the higher Algæ, and in all plants above the level of Thallophytes, only a *part* of the protoplasm of the plant-body is used in the formation of the reproductive cells. The rest must then eventually die. But in these lower forms, where all the protoplasm of the body is used in the production of new individuals, death, as a necessary event, can hardly be said to occur.

Gametes are formed in *Chlamydomonas* in exactly the same way as daughter individuals. They are, however, smaller and have no cell-wall. In one species at least the gametes are of two sizes. Of the smaller (*microgametes*) eight are produced from a parent individual, while only two of the larger size (*megagametes*) are formed from the parent cell. In the process of conjugation a microgamete and megagamete come into contact at their anterior colourless ends, the flagella are drawn in, and a thick cellulose membrane is secreted round the bodies of both. The protoplasm of the microgamete then passes over into the space inclosed by the part of the membrane belonging to the megagamete, and completely fuses with the protoplasm of the latter. A wall is then formed, cutting off the empty shell of the microgamete. The contents of the zygote eventually divides to form two or four new individuals which escape from its membrane. In the conjugation of most species where there is no distinction in size between the gametes, a cell-wall is only acquired *after* the foundation of the zygote. This is the regular course of events in the conjugation of the motile gametes of Green Algæ.

The genus *Sphœrella* resembles *Chlamydomonas* in the fundamental points of its structure. The main distinction is the existence of a considerable space separating the membrane from the main body of the protoplasm of *Sphœrella*. This space is bridged by fine strands of protoplasm, which radiate from the central mass and end in fine branches under the membrane. The anterior colourless protoplasm is drawn out into a beak, and to the extremity of this the two flagella are attached. The flagella often pass through two very delicate cellulose tubes, which in the common species, *S. pluvialis*, diverge from the extremity of the beak, and end on either side at the membrane. In another species (*S. Bütschlii*) the beak runs right up to the membrane, and the flagella-tubes, which are short and slightly curved, lie on the outer surface of the membrane.

Sphœrella pluvialis is a very well-known microscopic object, being extremely common in pools of rain-water. Its protoplasm often contains a good deal of the red

pigment hæmatochrome, which may almost completely mask its green colour. It was from this circumstance that it received its name of *Hæmatococcus pluvialis*. Hæmatochrome is even more constantly present in *Sphærella nivalis*, the "red snow", whose appearance and life-history have already been described (vol. i. p. 39). *S. Bütschlii* has its hæmatochrome concentrated in an eye-spot like that of *Chlamydomonas*.

The *Volvoceæ* differ from the *Chlamydomonadeæ* in consisting of motile colonies of cells, the members of each colony being united in a common investment. The bodies of the individuals composing the colony are also joined in some genera by protoplasmic processes. The body of each individual is identical, in the fundamental points of its structure, with that of a *Chlamydomonas* or of a *Sphærella*. The *Volvoceæ* present us with an interesting series of forms, showing a gradually increasing sexual differentiation of gametes, and, in the higher forms, an interesting subordination of the individual to the colony as a whole.

Gonium is a form in which the colony consists of (usually) sixteen *Chlamydomonas*-like cells arranged in a flat plate, which swims in a line at right angles to its surface, the flagella of the central cells of the disc projecting forwards, those of the peripheral cells obliquely outwards and forwards. All the cells are inclosed in a general mucilaginous envelope, and are joined to one another by protoplasmic processes.

Reproduction is effected by the division of the constituent cells of the colony in two planes at right angles to one another and to the plane of the colony, so that each mother colony produces sixteen daughter colonies, whose discs of cells all lie in the same plane. Meanwhile, the mother cells are separated from one another by the gradual liquefaction of the general mucilaginous envelope, and thus the daughter colonies become independent.

Formation of isogametes also takes place, but is not thoroughly understood.

Stephanosphæra is a very beautiful form, occurring especially in pools of rain-water collected in rock hollows in hilly districts. It is often found in company with *Sphærella pluvialis*. The colony consists of a ring of (usually) eight *Sphærella*-like cells arranged in the equatorial plane of a spherical or ovoid cellulose membrane.

When reproduction is about to occur, the constituent cells draw in the protoplasmic processes by which they are attached to the general membrane; each secretes a membrane of its own, and then its protoplasm divides in two planes to form eight (sometimes seven) daughter-cells. When these have acquired flagella they begin to swarm, and eventually escape by bursting the membrane of the mother colony.

Gametes are formed in the same way, but usually by more divisions, as many as thirty-two being sometimes produced from a single cell. In most cases all the cells of a colony divide at once to form gametes, but this is not invariably the case. Each bundle of gametes produced from a single cell breaks up, and all the gametes begin to swarm within the colony. The gametes are spindle-shaped, each with two flagella and an eye-spot. They conjugate in pairs, usually inside the general membrane, but conjugation never takes place between two gametes derived from the

same mother cell. The actual process of pairing has been fully described, and it may be taken as a type of the course of events, as it has been observed in all Algæ with isoplanogametes whose pairing has been fully investigated. Out of the crowd of gametes swarming in all directions, two approach and stroke each other with their flagella; in some cases the two separate and both become again lost in the crowd, but, when pairing is going to take place, they become firmly fixed together by their colourless anterior ends. The long axes of their bodies may then lie in one straight line, or may diverge at a wide angle. A rotation of each of the pairing gametes about its fixed anterior end now always occurs, the bodies becoming gradually approximated, so that their long axes come to lie nearly parallel. Fusion of the protoplasm follows, beginning at the already joined anterior ends, and progressing rapidly backwards till a single mass of protoplasm is formed. The four flagella still move actively, and the *Zygozoospore*, as this active type of zygote is often called, escapes from the general membrane of the mother colony, becomes spherical by shortening of its long axis, loses its flagella, and puts on a cell-wall. The protoplasm soon loses its green colour, becoming reddish, and the zygote enters on a resting period. Eventually its protoplasm divides, producing zoospores, each of which gives rise to a new colony.

The division of the cells of a colony to form zoospores or gametes begins in the evening, and is finished soon after sunrise. In dull weather, however, its completion is delayed far into the day. This dependence of the formation of zoospores and gametes upon the influence of light, if not invariable, is found very widely among the Green Algæ.

Pandorina is a fairly common form in ponds, &c. The colony consists of sixteen wedge-shaped cells arranged in a sphere, and covered by a general investment, which is of considerable density at its external surface. The apex of each wedge is directed towards the centre of the sphere, and there is little space left between the adjacent cells. The formation of daughter-colonies is similar to that obtaining in *Gonium* and *Stephanosphæra*. The young colonies escape by liquefaction of the investing membrane. Colonies of gametes are formed in the same way, but often consist of eight instead of sixteen cells, and the acquirement of flagella and liquefaction of the mother membrane takes place more slowly. Eventually the membrane of each gamete-colony also becomes liquefied, and most of the gametes swarm out into the water. A great number of mother colonies of different sizes simultaneously take part in this production of gametes, so that the water becomes filled with masses of swarming gametes of very variable dimensions. No distinct size-categories are, however, to be distinguished. Conjugation now takes place between pairs of gametes either of the same or of different sizes; with this exception, that the largest gametes do not fuse with one another. They are relatively inactive, sometimes, indeed, remaining fixed in their colonies, and are sought out and paired with by the smaller and more active individuals. Here, then, we have a most interesting stage in the evolution of sex. The largest, relatively passive, gametes may fairly be called female, while the different sizes of smaller

gametes, though not sexually differentiated *inter se*, since conjugation is apparently possible between any two, whatever their relative size, may perhaps be considered as male in relation to the largest.

It is probable that fully-differentiated male and female gametes arose from forms such as we find in *Pandorina*, by the suppression of the intermediate sizes, the smaller and more active gametes taking on the function of actively seeking out the larger passive individuals, which on their side contribute practically the whole of the stock of food required by the zygote in germination. In correspondence with this we find the chromatophore (chlorophyll-corpuscle), which may be considered as the specially food-producing organ of the algal cell, much reduced and eventually functionless or absent altogether in the more highly differentiated male gametes (*spermatozoids*).

Eudorina has a colony of sixteen or thirty-two almost spherical cells considerably separated from one another, and inclosed in a general investment like that of *Pandorina*. In the production of daughter-colonies *Eudorina* resembles the lower forms of the volvocine series, but in the sexual differentiation of the gametes there is a decided advance upon that obtaining in *Pandorina*. The perfectly passive female gametes (oospheres) hardly differ from the ordinary cells of a vegetative colony, while the active male gametes (spermatozoids) are formed in bundles of sixty-four by successive divisions of similar cells. Here, then, we find the marked difference in size between the two categories of gametes brought about, as it very often is among the Algæ (and, indeed, among many other plants and animals), by a marked difference in the number of divisions occurring in their respective mother-cells. The present case in which strictly comparable cells on the one hand directly give rise to eggs, and on the other divide to form sixty-four spermatozoids each, is rather extreme, but we have already met with a similar case in a species of *Chlamydomonas*.

Each spermatozoid of *Eudorina* is club-shaped, with a colourless pointed anterior end bearing two flagella and possessing an eye-spot, and a yellowish thick posterior extremity representing the (reduced) chlorophyllous portion of the typical volvocine cell. The spermatozoid bundle (male colony) escapes from its mother-cell-membrane, and swarms as a whole towards a female colony. On reaching the latter the spermatozoids get their flagella, become entangled in the thick mucilage, and rapidly separating from one another, worm their way into the female colony. Some succeed in fusing with the individual female gametes, and each zygote thus formed will eventually give rise to a new *Eudorina* colony.

A form recently discovered almost at the same time in three different States of North America, and known as *Pleodorina*, shows an important difference from the types we have hitherto been considering. Each spherical colony consists of about 128 cells, but not all of these are capable of producing daughter-colonies. This power is confined to those cells which occupy the posterior half or two-thirds of the sphere (it should be explained that the colony moves forward in relation to a definite axis). The smaller anteriorly-placed cells are thus purely vegetative in

function, and necessarily die after the reproductive cells have given rise to daughter-colonies. This is the first time we have met with such natural death among the Algæ, and it is very clearly seen to be connected with the separation of the assimilative and reproductive functions. The formation of gametes in *Pleodorina* has unfortunately not yet been observed.

The remarkable and beautiful organism called *Volvox* has been known for more than two centuries, and has long been among the most favourite of microscopic objects. The purely scientific interest which it has aroused has been as great as the æsthetic admiration which it has excited. Long and animated controversies have raged on the question as to whether it was to be regarded as an animal or a plant, as an individual or as a colony of individuals. And although these questions have now lost much of their actuality through the gradual recognition by naturalists that we have absolutely no criteria by which they can be settled, there have arisen problems which promise quite as much interest and excitement for the future.

Volvox is much larger than the forms hitherto described. The colony is spherical, and possesses a single layer of cells on its surface. In *V. Globator* the sphere may be over a millimetre in diameter, but more usually its diameter is only some three-quarters of a millimetre. A particularly large specimen may possess as many as 22,000 cells (10,000 is a more usual number). Many of the cells, however, as in *Pleodorina*, are simply vegetative, and take no part in the reproduction of the colony. Usually, in fact, only a very small minority of the cells are reproductive.

The two species of *Volvox* differ from each other in a great number of points, but we have only space for a very brief description of some of the most interesting.

The cells of *Volvox Globator* are all united together by very stout processes. Each cell, which is inclosed in a separate cell-wall, possesses all the ordinary features of the *Chlamydomonas* type.

Daughter-colonies are developed from special cells, usually eight in number, called *parthenogonidia*. They are always formed in the posterior part of the mother-colony, early becoming larger than the ordinary vegetative cells. Each divides repeatedly, and forms a hollow sphere of closely-packed cells, which, after the last division, mostly acquire the characters of the adult vegetative cells, the remainder gradually increasing in size to form the reproductive cells. The young colonies then escape from the mother, apparently by pushing themselves against and making rents in its posterior wall. Subsequently the cell-membranes swell a good deal, separating the cell-bodies from one another, and the colony attains its adult size.

In other cases gametes may be formed in a young colony. About five cells (*androgonidia*), strongly resembling the parthenogonidia, divide to form discs or hollow spheres of a hundred or more spermatozoids. The spermatozoids resemble in a general way those of *Eudorina*, but are peculiar in having the pair of flagella inserted laterally at the base of the colourless beak and near the eye-spot. In the

same colonies, but a little later than the androgonidia, about thirty much larger spherical cells, the oospheres, are developed, and these are duly fertilized, but by spermatozoids derived from another colony. The zygote has a sculptured exine. Parthenogonidia are not found in those colonies which produce gametes.

Volvox aureus (= *V. minor*), the commoner form, is usually much smaller than *V. Globator*, and has rounded cells more widely separated and connected by very delicate processes. But perhaps its most striking characteristic is the very great variability in the number and distribution of the reproductive cells. The parthenogonidia, which vary in number from one to sixteen, may either occur alone or in one colony with androgonidia or oospheres, or both. Most of the sexual colonies are dicœcious, though this is not always the case. The colonies containing androgonidia unaccompanied by other reproductive cells often develop very numerous (up to 1100) spermatozoid bundles, the androgonidia forming one-third of all the cells of the colony. The spermatozoids differ from those of *V. Globator* by their larger size, by their terminal flagella at the end of a shorter beak, and by the possession of a well-developed leaf-green chromatophore. We must, therefore, consider *V. aureus* as not so highly developed, in some respects at least, as *V. Globator*.

A *Volvox*-colony always swims in the direction of a given axis passing through its body, and at the same time rotates to the right or left about an axis which is inclined obliquely to the antero-posterior axis. The eye-spots of the vegetative cells are much better developed in the anterior half of the colony, and are always situated on the side of the cell nearest the anterior pole. These facts tend to support the view of the function of eye-spots in general suggested in page 629.

Volvox stands at the head of the series of colonial (cœnobe-forming) organisms which we have been tracing, a series diverging from a *Chlamydomonas*- or *Sphærella*-like type, and whose successive forms gradually increase in size, complexity, and sexual differentiation. *Volvox* itself has been well spoken of as "the culmination of Nature's attempt to evolve a higher organism out of a cœnobe". It was an attempt which failed, or rather which could not be carried any further than *Volvox* itself. A delicate, easily-ruptured *Volvox*-sphere could certainly not continue to exist if it were much more than a millimetre in diameter. As it is, the wall is often split, and all sorts of smaller organisms get inside, resulting in the more or less speedy collapse of the *Volvox*-colony.

But there are other series diverging from the Chlamydomonadeæ, and some at least of them have followed lines on which it was possible for higher and more varied plant-forms to be developed.

At the first stage along one of these lines of descent we find ourselves among forms in which the dominant phase of the life-history falls in a resting stage, either fixed or freely floating in the water. From this resting stage motile forms (zoospores), corresponding with the free-swimming *Chlamydomonas* individuals, are directly developed. These zoospores, after a short period of swarming, come to rest, often fixing themselves by their anterior end to some solid object. With little or no change in the constitution and appearance of the cell the main portion of the

life cycle is passed in this fixed condition, and cell divisions take place, the products eventually again developing flagella and being set free as zoospores. The genera *Chlorangium* and *Physocytium* are examples of the simplest form of this type of life-history. Forms with a rather more complicated structure in the fixed stage are found in the genera *Mischococcus* (a common form on the surface of threads of the higher Algæ), *Euglenopsis* (a newly-discovered American plant), and their allies. In these the protoplasm of the zoospore, after fixing itself and putting on a delicate cell-wall, pushes out the surface of its membrane away from the substratum, thus forming a tube of gradually increasing length, the apex of which is always occupied by the protoplasm. Division of the protoplasm and subsequent pushing out of the wall of the tube in different directions by the daughter-cells results in a branching of the hollow stalk, and in this way quite a considerable branching plant-body may be produced. Eventually some or all of the cells occupying the apices of the various branches of the tube acquire flagella and escape into the water as zoospores, which again settle on solid objects and give rise to new plants.

Other forms in which the cell derived from a zoospore multiplies by division, the products eventually again giving rise to zoospores, are *Schizochlamys*, *Botryococcus*, *Dictyosphærium* and *Tetraspora*. In these, however, the immotile phase is not fixed, but forms floating colonies of various conformation. Into this topic we cannot enter further, except to remark that *Tetraspora* forms flat colonies of cells arranged in one plane and held together by the swollen mucilaginous cell-walls. Cell division takes place in planes at right angles to that of the colony. This type of colony is specially interesting, as it suggests the form of thallus found in *Ulvaceæ*, which in turn appears to lead on to the higher forms *Confervoideæ*.

Pleurococcaceæ.—More or less closely allied to the above-mentioned genera are others which do not form zoospores at all. These types with no motile phase in their life-cycle may be conveniently classed together as *Pleurococcaceæ*. The type-genus *Pleurococcus* contains some of the most widely-distributed algal forms known. *P. vulgaris* forms the bulk of the green coating of damp earth, tree trunks, palings, &c., in all regions of the globe. It consists of roundish cells, dividing in three directions in space and thus forming solid masses of cells hanging together in multiples of two, and often flattened by lateral contact. Each cell contains several parietal chromatophores which may, however, fuse together to form a single one. Resting akinetes are formed by the cells ceasing to divide, becoming spherical, and thickening their walls. At the same time oil appears in the protoplasm. It is probably mainly in this phase that *Pleurococcus* gets distributed by the wind from one place of growth to another. Owing to the resemblance of the akinetes of some of the confervoid Algæ to those of *Pleurococcus*, it has often been stated, and indeed is still held by some algologists that *Pleurococcus* itself is merely a growth-phase of these higher Algæ. But recent culture-experiments leave little room for doubt that *Pleurococcus* is a perfectly autonomous form, although it may often be associated with pleurococcoid stages of other Algæ. *Eremosphæra* is a pretty form, common in fresh water, with single floating spherical cells. Each cell contains numerous separate chlorophyll-

bodies, embedded in a parietal layer of protoplasm, and a nucleus suspended by protoplasmic strands in the centre of the cell. Multiplication is effected by division of the protoplasm into two daughter-cells which escape by rupture of the mother-cell membrane. *Scenedesmus* is another motionless floating fresh-water form. It consists of oblong cells united into groups of two, four, or eight, which lie side by side, palisade fashion. Some or all of the cells often possess straight or horn-like projections of their walls, which give the cell groups a very characteristic appearance. The single solid chromatophore occupies nearly the whole cell cavity. *Chlorella* is a genus whose cells are symbiotic with *Radiolaria* (yellow cells). Other forms live in a similar relation with certain Cœlenterates and Platyhelminths. Several help to form lichens. Since the various genera of *Pleurococcaceæ* differ thus very widely in the form and structure of their cells, and indeed are only united by the negative character of the absence of zoospores, it is almost certain that they cannot be considered as forming a natural group. The various genera are very probably allied to different neighbouring groups from which they have been derived by the suppression of the habit of forming zoospores.

The *Endosphæraceæ* are a small and very natural group of unicellular Algæ, characterized by their habit of living in the intercellular spaces of various higher plants. They possess motile zoospores, or gametes, or both, but the motionless cells produced from these do not undergo vegetative divisions. Very possibly they represent a separate line of descent from the Chlamydomonadeæ, a line of descent in which the motionless cell has become the dominant phase in the life-cycle, and has been specially adapted to the new conditions of life, but differs from the motionless cells of the "Tetrasporaceæ" in directly forming zoospores without undergoing purely vegetative divisions.

Two forms of Endosphæraceæ may be taken as illustrations of this type of life-history.

Chlorochytrium Lemnæ inhabits the intercellular spaces immediately under the epidermis of the leaves of *Lemna trisulca* (the Ivy-leaved Duckweed). Each plant consists of a single, thick-walled, oval cell with a parietal chromatophore containing numerous pyrenoids and a large central vacuole. Very numerous pear-shaped isogametes are formed by successive divisions of the protoplasm of the cell. Then a layer of substance outside the mass of gametes (probably the ectoplasm of the cell) begins to swell strongly, and bursts not only the cell-wall but also the superincumbent tissue of the Duckweed leaf, forming a sphere of mucilage in which the gametes begin to swarm and to conjugate in pairs. Spherical zygozoospores are thus produced; these escape from the mucilage, and after some free swarming in the surrounding water, settle on the boundary between two epidermal cells of a Duckweed leaf, draw in their flagella, put on a cell-membrane, and form a definite parietal chlorophyll-body with a single pyrenoid. After two or three days a delicate, colourless tube is put out, which forces its way between the two epidermal cells of the leaf, and reaches an intercellular space. The contents of the zygote slowly pass over into the apex of this tube, which gradually increases in size and assumes the

characters of a young vegetative cell, the original zygote-wall remaining on the surface of the leaf as a mere cellulose knob.

The generations rapidly succeed one another during the summer months, the last-formed cells of the season becoming packed with starch grains and passing the winter in this state. These resting cells can withstand desiccation, in case the pond in which the duckweed lives becomes dried up.

Phyllobium dimorphum forms large immotile cells between the tracheids of the vascular bundles in the leaves of the creeping Moneywort (*Lysimachia nummularia*). This plant lives in damp woods and other shady places. The Rhine plain in the neighbourhood of Strasburg, where *Phyllobium* was first found in the leaves of the Moneywort, is usually flooded during the month of June, partly by the rising of the river, and partly by the thunderstorms which usually occur about that time of the year. The *Phyllobium*-cells take this opportunity to form their gametes, which are of two distinct sizes, each cell producing gametes of one size only. After the escape of the gametes into the surrounding water conjugation occurs. The zygozoospores produced have only two flagella, the body and flagella of each microgamete being completely lost in the megagamete, just as the body of a spermatozoid is completely lost in the substance of the egg. After coming to rest on the surface of a Lysimachia leaf, and acquiring cell-membranes, the zygotes put out delicate tubes which enter the stomata of the leaf. If a leaf is infected by a few zygotes only, the tubes formed reach the vascular bundles, and forcing their way between the elements of the wood, grow forward in the bundles, branching when they branch, and attaining to a considerable length. Eventually, towards the end of the summer, the protoplasmic contents of each tube becoming concentrated in one spot, this part of the tube swells and is cut off from the remainder by the formation of transverse partitions. The swollen part of the tube thus forms a large cell which rests during the winter, and in the next summer will produce gametes. If, on the other hand, the leaf is infected by a large number of zygotes, most of the tubes never get any further than the intercellular spaces immediately under the stomata. In this position they form small resting cells in large numbers. These eventually form *zoospores*, which apparently behave, on germination, just like the zygozoospores. The dimorphism of the resting cells of *Phyllobium* thus depends directly on the *amount of space* at the disposal of the germ tubes. This conclusion can be confirmed by cultivating the germ tubes apart from the leaves of the host.

The purpose of the germ tubes of *Chlorochytrium*, *Phyllobium*, and their allies in penetrating the leaves of their hosts, seems to be simply that they may gain the advantage of a quiet protected place for their development. Just in the same way Diatoms and other unicellular forms often live comfortably in the empty cells of Algæ, the intercellular spaces of the Bog-moss (Sphagnum), and similar situations. Only in the case of these Endosphæreæ the association of the Alga with its habitat is invariable and adaptive, not merely casual and unrelated. But the Endosphæreæ are not parasites in any sense. They take no food from their "hosts" nor do they exercise any appreciable influence on the latter. This is sufficiently proved by the

fact that *Lemna trisulca* lives quite happily and can flower when infested with *Chlorochytrium*, and that the germ tubes of *Phyllobium dimorphum* usually enter dead leaves of the Moneywort. Another form which always enters the living leaves of a river-weed, continues its course of development whether the leaves die or remain alive. It is not, however, difficult to imagine how a form like *Phyllobium*, living as it does in the vascular bundles of its host, might acquire a parasitic habit by tapping the food supplies. As a matter of fact certain confervoid Algæ are known whose presence results in the death of the leaves they inhabit, though probably not by direct appropriation of the food of the host.

Resembling the *Endosphæreæ* in possessing motionless cells which form zoospores but do not undergo vegetative divisions, are certain common fresh-water forms of which *Characium* and *Sciadium* may be mentioned. A plant of *Sciadium* originally consists of a single cylindrical cell whose contents breaks up into zoospores. These zoospores have acquired the peculiar habit of settling on the rim of the mother-cell, instead of seeking out fresh spots for their development. Each zoospore produces a single cell like the mother, so that a whorl of cells of the new generation is formed on the top of the original cell. This process may be repeated for two or three generations, after which the zoospores will settle on some other object and start fresh "plants".

The *Hydrodictyaceæ* are a group of Algæ which form immotile colonies. The cells of these colonies resemble the single cells of the forms we have just been considering in producing zoospores or gametes, but undergoing no vegetative divisions. The colony is formed by the joining together in a definite way of the group of zoospores formed in a single cell of the mother-colony. Each of these zoospores then develops into an adult vegetative cell.

The recently discovered genus *Euastropsis* (so called from its likeness to the Desmid *Euastrum*) is the simplest type of the family. It consists of two mitre-shaped cells joined to one another by their bases. Each cell contains a parietal chromatophore with a single pyrenoid, and a single nucleus. The contents break up by successive divisions into 2–32 zoospores, which escape from the cell surrounded by a general membrane. After oscillating for about a quarter of an hour, the zoospores become attached in pairs by their anterior ends. Each pair then takes on the characters of the two-celled colony.

Pediastrum (fig. 370 [6]) consists of a disc of cells, of which the marginal ones are often drawn out into lobes or processes. The chromatophore is parietal with a single pyrenoid; there are numerous nuclei. The formation of zoospores is like that of *Euastropsis*, but their movement is more lively, and eventually all the zoospores formed in a single cell join together to form a new *Pediastrum*-colony (figs. 370 [7] and 370 [8]). Gametes are formed in the same way as the zoospores, but are smaller and more numerous. They escape from the investing membrane, swim freely in the water, and fuse in pairs to form zygotes. From these zygotes new *Pediastrum*-colonies are produced indirectly, probably by a method like that obtaining in *Hydrodictyon*.

Hydrodictyon, the Water-net (figs. 370[1] and 370[2]) is a beautiful organism forming net-like colonies of cylindrical cells, which are joined end to end, forming the sides of the polygonal meshes. Each cell may be as much as 1 centimetre in length. A thin layer of protoplasm containing numerous small nuclei lines the wall and incloses a large central vacuole. The chromatophore, or chlorophyll-layer of the protoplasm, contains many pyrenoids, each surrounded by a sheath of starch grains. Fine-grained starch is also scattered through the substance of the chro-

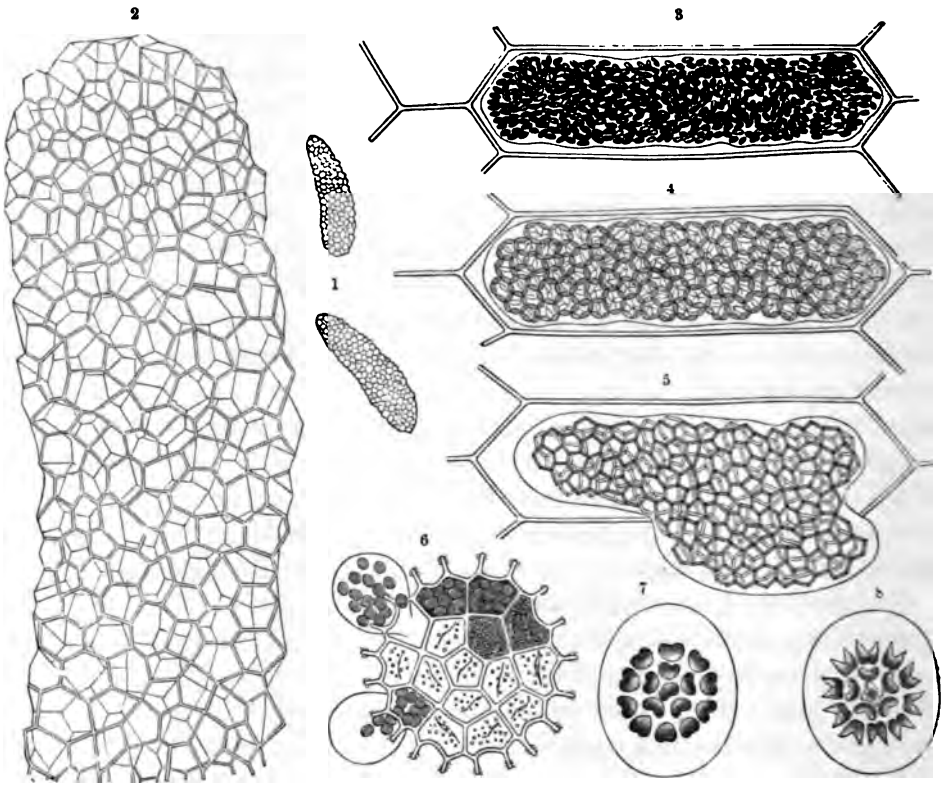


Fig. 370.—Hydrodictyaceæ.

[1] The Water-net (*Hydrodictyon utriculatum*), nat. size. [2] A portion of the same magnified 50 diameters. [3], [4], and [5] Formation of zoospores in a cell of *Hydrodictyon*, showing their union together, and escape as a young net; × 300. [6] *Pediastrum granulatum*; development and escape of zoospores, the lightly-dotted chambers already vacated. [7] and [8] Zoospores after their escape arranged as a new *Pediastrum* plant; × 240.

matophore. This stroma-starch appears in great quantity when growth is checked and assimilation remains active, disappearing again if assimilation is stopped. The pyrenoid-starch, on the other hand, seems to be withdrawn from the ordinary metabolism of the cell, since it is formed round each pyrenoid early in the life of the cell, and remains there under all circumstances, unless the cell is on the point of actual starvation in the dark, till the onset of reproduction. When zoospores are about to be formed the pyrenoids together with their starch disappear, and abundant stroma-starch appears. At the same time the nuclei multiply a good deal by division, and eventually the whole of the protoplasm divides to form a great num-

ber of zoospores. These zoospores, however, never become free like those of *Pediastrum*, but remain joined together by strands of protoplasm, and after a certain amount of shifting backwards and forwards, come to rest with their ends in contact. Each then gradually assumes the characters of a *Hydrodictyon*-cell, the young colony eventually escaping from the mother-cell (figs. 370 [3, 4, 5]). Gametes are formed in the same way as zoospores, but are smaller and more numerous. The spherical zygote gradually increases in size, and its contents breaks up into 2–5 large zoospores, which develop into large cells with pointed processes, the so-called *polyhedra*. In the interior of each polyhedron an embryonic *Hydrodictyon*-net is developed from swarm-spores, and in the cells of this ordinary *Hydrodictyon* colonies are found.

It has been shown experimentally that any *Hydrodictyon-net* above a certain size and age is capable of producing either zoospores or gametes, and that the stimulus to the formation of one or the other is given by external conditions. Thus bright light, fresh water rich in inorganic nutritive salts, and fairly high temperatures, are favourable to the production of zoospores, while the reverse of these conditions, and especially the presence of organic substances, such as sugar, tend to make the cells of a net produce gametes. The conditions favourable to zoospore-formation are also of course, favourable to active vegetative growth, and no doubt the abundant formation of new protoplasm is a necessary preliminary to the production of zoospores. A slight check to the processes of assimilation and growth is apparently necessary in order to give play to the zoospore-forming forces. Thus, experimentally, a change from a strong solution of nutritive salts to fresh water will induce the formation of zoospores in nets which would simply have gone on growing if left in the nutritive solution. A similar check is probably given by the waning light in many Algæ in which zoospores are produced at night. For the production of gametes, on the other hand, an actual reversal of the conditions favourable to growth is necessary. In nature this probably happens when by very active growth the whole of the water of a pool is filled with nets, the inorganic food and oxygen are exhausted, and the normal chemical processes of the cell receive a check. The formation of gametes and zygotes under these conditions is obviously adaptive, since the zygote can, although it need not, rest during several months till the conditions are quite altered. We may therefore conclude that, whereas zoospores are especially designed to multiply and distribute the species, zygotes are intended to preserve it under unfavourable conditions. It is probable that the production of large zoospores and polyhedra is a necessary part of the life-cycle following the germination of the zygote, and cannot be altered by the incidence of different conditions.

Alliance VII.—Siphoneæ.

Thallus consisting of a tube, often much branched, and containing many nuclei. This tube is the production of a single cell, but in the more complicated forms is often shut off into compartments by transverse septa. Reproduction by zoospores

and planogametes, or spermatozoids and eggs: in very many forms no reproductive cells are known. The higher forms of Siphoneæ often produce plant-bodies of very definite and characteristic external form, and of considerable size. In some cases these simulate the external form of various higher plants.

Families: *Botrydiaceæ, Phyllosiphonaceæ, Vaucheriaceæ, Bryopsidaceæ, Caulerpaceæ, Codiaceæ, Valoniaceæ, Verticellatæ.*

Botrydiaceæ.—*Botrydium granulatum* is a little plant found growing especially on loam at the damp edges of ponds and ditches. It consists of a club-shaped or balloon-shaped green shoot-portion, about 1–4 millimetres in diameter, continuous with a simple or branched tubular colourless root-portion which is embedded in the substratum. The entire plant consists of a single cell, that is to say, its cavity is continuous throughout. The wall is lined with a thin layer of protoplasm, which contains many nuclei, and, in the shoot, a net-like chlorophyll-layer.

Botrydium can reproduce itself in very various ways, according to the incidence of external conditions. The simplest form of propagation is by budding, which takes place under conditions favourable to the ordinary vegetation of the plant. The shoot-portion of a small vegetative plant sends out a process which swells to the size of the mother shoot, puts out a colourless root, and is then constricted off to form a separate plant. But if the plants are covered with water they cannot go on growing comfortably, and accordingly the protoplasm breaks up to form a number of zoospores, each with a single flagellum and two lateral chromatophores. The mass of zoospores is subjected to considerable pressure by the swelling up of a ring-like area of the wall, and the tension becomes so great as to rupture the wall in the centre of the ring and expel the mass of zoospores into the water. On damp soil the zoospores come to rest, and germinate to form new plants. If a zoospore cannot escape from the water it enters on a resting stage, which gives rise to a new plant directly it finds itself on damp soil. Further, if a young plant is exposed to bright sunlight, its protoplasm breaks up into a number of spherical cells, each of which puts on a cell-wall. If now these spherical cells (*gametangia*) are placed in water, the contents of each breaks up into spindle-shaped, biflagellate gametes, which conjugate in pairs to form zygotes. These zygotes can rest for a longer or shorter time, but if placed on damp earth they at once germinate to form new plants. If, on the other hand, the gametangia are placed in water after being kept for two years they give rise to biflagellate cells which rather resemble the gametes, but which on damp soil germinate directly to form vegetative plants. Finally, if the gametangia are at once placed on damp soil, their contents does not break up, but the whole gametangium germinates and produces a plant. Supposing a large *Botrydium*-plant, with a balloon-shaped shoot, be exposed to insolation (bright light) its contents, instead of forming gametangia, travel down into the root, and the protoplasm there divides to form rows of *root-cells*, each with an independent cell-wall. If a root containing root-cells be placed in water, the protoplasm of each cell breaks up into a number of zoospores: if the root be placed on damp earth each

root-cell sends out a tube which grows into a young vegetative plant: if left in the soil, the latter remaining damp, each root-cell germinates to form a peculiar thick-walled plant called a *hypnosporangium* which can withstand desiccation, and which in water gives rise to a number of zoospores.

The above facts may be briefly expressed by saying that any stage in the life-history of *Botrydium* tends (1) on damp soil to form vegetative plants, (2) in water to form zoospores or gametes, (3) in dry conditions to form resting cells. There can, then, be no doubt that here, as in the case of *Hydrodictyon*, we are justified in saying that the form which any given set of conditions tends to produce is adapted to meet those conditions.

Phyllosiphonaceæ.—*Phyllosiphon Arisari* is an Alga living in the intercellular spaces of the leaves of *Arisarum vulgare* in Southern France and Italy. Its thallus consists of a much-branched tube, the parietal protoplasm containing many nuclei and small disc-shaped chromatophores. Unlike the *Endosphæreæ*, the presence of *Phyllosiphon* has a considerable effect on its host, causing blotches of dead tissue to appear in the leaves. As the Alga can presumably assimilate quite well for itself, this destruction of tissue is probably caused by withdrawal of water from the cells of the host. The only kind of reproductive cells which *Phyllosiphon* is known to produce are aplanospores (non-motile spores). These are formed by the division of the whole of the protoplasm of the thallus. They are extruded by the swelling of the inner membrane of the tube which bursts the outer membrane just under a stoma, shooting out a jet of mucilage in which the aplanospores are embedded. The latter germinate directly, the germ-tubes entering the leaf between two epidermal cells.

Vaucheriaceæ.—This family includes only the well-known and widely distributed genus *Vaucheria*. Different species of *Vaucheria* grow in brackish and fresh water, both running and stagnant, or in the air in damp situations. The thallus consists of relatively coarse branched tubes, quite visible to the naked eye. The interior of the tube is lined by a layer of protoplasm containing numerous disc-shaped chlorophyll-grains and many nuclei. The *Vaucheria*-plant is fixed to its substratum by short-branched, colourless processes, but, except in connection with the formation of reproductive cells, transverse septa are not formed in the tubes.

The gametes of *Vaucheria* are formed in special organs, known as antheridia and oogonia. The distinction of sex is very strongly marked, the male gametes or spermatozoids being very small oval cells, each with two laterally inserted flagella, while the female gametes or eggs are very large and quite motionless. The antheridia are often spirally curved branches of the main tube, a transverse wall separating the upper part of the spiral, the antheridium proper, from the lower part, which is continuous with the cavity of the vegetative tube. Sometimes, however, the antheridium is straight and club-shaped, and in other cases it may be separated from the main tube by an intermediate cell. The thirty-five species of *Vaucheria* are classified according to the characters of their antheridia. The oogonia are

ovoid or spherical, and usually possess a lateral beak. While the antheridium produces a large number of the small spermatozoids, the oogonium gives rise to a single large egg. An account has already been given of the process of fertilization (see p. 58, and figs. 204[5] and 204[6], on p. 53).

Vaucheria also produces peculiar zoospores, whose development and subsequent behaviour have been described on pp. 23 and 24 of vol. i. (see Plate I. a–d). The cilia with which the surface of the zoospore is clothed are arranged in pairs, and in the colourless external layer of protoplasm just below each pair of cilia is situated a single nucleus. This suggests that the zoospore of *Vaucheria* is to be regarded as really equivalent to a great many zoospores which have not separated during development, each nucleus, with its pair of cilia and a certain amount of chlorophyll and protoplasm, representing an ordinary zoospore. It has been found that if, as often happens, the zoospore breaks into two during its struggles to escape from the end of its tube, the front part rounds itself off and swims away, behaving just like an entire zoospore. In some species of *Vaucheria* the zoospores are only partially clothed with cilia and come to rest soon after their escape. In yet others they have no cilia at all, and either escape by dissolution of the end of the tube, or germinate *in situ*. Here then we have a transition from the formation of active zoospores to the production of passive aplanospores.

The occurrence and form of reproduction is here even more entirely under the control of conditions than is the case in *Hydrodictyon*. The age and size of the plant are no longer factors, since sexual organs and zoospores can be formed on quite short germ-tubes. Cultivation of the plant in a solution rich in inorganic food-salts always gives it a tendency to produce zoospores, but the immediate stimulus to their formation is given by a distinct *change* in the conditions, just as is the case in the Water-net. In *Vaucheria* this change is especially necessary, since each zoospore is formed in the apex of a tube, and apical growth must be stopped in order to allow free play to the zoospore-forming forces.

The nature of the change, so far as regards the medium, is apparently immaterial—it may be a change from running water to still water, or from a damp atmosphere to water, or in the temperature or concentration of the culture-solution, but it is a change from light to darkness which is especially effective. This is quite contrary to the case of *Hydrodictyon*. The presence of water and a temperature between 3° and 26° C. are absolutely necessary conditions of zoospore-formation.

The former condition is obviously adaptive. The formation of sexual organs is specially induced by the replacement of inorganic salts by organic substances (*e.g.* sugar), just as in the case of the gametes of *Hydrodictyon*, but antheridia and oogonia, which are formed much more frequently and easily than are the Water-net gametes, often appear in the presence of salts, and when growing in a damp atmosphere. Light and a temperature above 3° C. are absolutely necessary conditions.

The most striking point in the physiology of the reproduction of *Vaucheria* is the prominent part played by the sexual organs. These are undoubtedly the principal means of propagation the plant possesses, the zoospores, which usually fulfil this

rôle, having fallen to a subordinate position. Only in forms like *Vaucheria clavata*, adapted to life in rapidly-flowing water, have the zoospores a primary importance. Sexual reproduction is here difficult, and zoospores are always produced in abundance on the slightest change of conditions.

Bryopsidaceæ.—This family consists of marine, mostly tropical, forms. The plant-body of *Bryopsis* has quite a definite form, and consists of a tube forming the main axis, fixed below by short root branches, and bearing above in acropetal succession a series of branches, some of unlimited, some of limited growth. In these latter are formed swarming cells which are of two sizes, the smaller being yellowish, while the larger have each a green chromatophore. It seems very probable that these are anisogametes, but their conjugation has not been observed.

Derbesia is a genus like *Bryopsis* in many respects, but with special zoosporangia which produce curious zoospores, each with an anterior crown of cilia.

Caulerpaceæ.—The genus *Caulerpa* contains nearly one hundred species, which present the most varied external forms, simulating those of many of the higher plants, such as Mosses, Ferns, Mare's-tails, Cactuses, Conifers, &c. Each plant, however, consists simply of a single much-branched but uninterrupted tube, the branches taking the forms of roots, leafy shoots, &c. The tube is supported internally by a complicated system of "beams" of cellulose which run out from the walls.

The Caulerpas live mainly in tropical and subtropical seas. They often grow together in large masses, forming great beds of sea-weed, their creeping stems or "rhizomes" extending many yards. No reproductive cells have as yet been found in any of them, multiplication taking place apparently solely by the breaking off of parts of the thallus, which drift and fix themselves elsewhere.

Codiaceæ.—Under this name we may conveniently place together a group of forms specially characterized by a thallus consisting of richly-branched tubes, which are interwoven to form a mass of more or less solid character, which possesses in each genus a definite and characteristic external conformation. Thus, *Penicillus* has a long cylindrical "stalk" fixed below by "rhizoids" and bearing above a head of free dichotomously branching radiating filaments. The older parts of the stalk are strongly incrusted with calcium carbonate.

Udotea has a stalk often creeping and branching, bearing flat fan-shaped fronds. Spherical bodies, the nature of which is unknown, are borne on short side branches of the tubes of which the frond is built up. *Halimeda* possesses a thallus mainly composed of series of heart- or kidney-shaped segments, which give many of the species the appearance of an *Opuntia*. There is usually a considerable deposit of calcium carbonate covering the thallus. Roundish structures, produced in grape-like bunches on the edges of the segments, liberate swarming cells whose behaviour has not been followed.

Codium has no well differentiated stalk or segments; the thallus is very various in form, and is differentiated into a well-marked pith and cortex, the tubes being mainly longitudinal and loosely packed in the former, while the latter consists of club-shaped closely-packed branches arranged at right angles to the surface. In

certain branches of the latter swarmers of two sizes are produced. Analogy would lead us to suppose that at least the smaller of these are gametes, but their behaviour has not been observed. Some species of *Codium* (e.g. *C. tomentosum*, with a dichotomously branched furry thallus) occur on our own coasts. The remaining Codiaceæ are largely tropical, but very widely distributed.

Valoniaceæ.—We may include in this family an assemblage of genera whose thallus consists of a branching tube, usually forming transverse walls, but with no interweaving of the branches such as we get in Codiaceæ.

The simplest type is found in *Valonia*, a form which at first consists of a single club-shaped cell, which produces a whorl of branches at its upper end. Each of these may again produce a whorl of branches of the second order.

A group of very beautiful genera form leaf-like structures, the branching of the thallus taking place in one plane. *Struvea* consists originally of a single cell, which grows apically and becomes divided by transverse walls into a series of segments. Each of these segments bears a pair of branches coming off right and left, and each branch behaves like the main axis. The secondary and tertiary branches thus produced come into contact, fixing themselves one to another by means of curious little rosette-like organs called *tenacula*, and the whole thus forms a net-like structure with larger or smaller meshes between the branches. The definite usually oval form of the "leaf", of which the main axis forms the midrib, and the primary branches the principal veins, is due to the latter, after they have attained a certain length, ceasing to produce branches on the side towards the base of the thallus, and at the same time bending forwards and inwards to join the primary branch next in front.

Struvea delicatula sometimes lives in the tissue of a Sponge belonging to the genus *Halichondria*. There is a reciprocal effect on the form of the two organisms, the Alga only taking on the characteristic *Struvea*-form when part of its thallus grows out clear of the body of the Sponge. In consequence of this it was for some time not suspected that this sponge-inhabiting Alga had any connection with *Struvea*. Neither organism seems to suffer from the association, and there is some evidence for regarding it as a case of true symbiosis.

Anadyomene is another very beautiful form resembling *Struvea* in the construction of its thallus, but with no meshes between the cells. It consists of two kinds of cells, the more elongated form the "ribs" of the thallus, the smaller and more rounded make up the intermediate tissue.

The genus *Boodlea*, in which the branching takes place in more than one plane, forms a transitional form connecting these genera with *Cladophora*, which is usually regarded as belonging to the Confervoideæ.

Verticillatæ.—In this group of the Siphoneæ the thallus consists of a long cylindrical undivided stalk, fixed below by rhizoids, and bearing above acropetal whorls of simple or branched appendages of limited growth. In some of these appendages gametes may be produced; zoospores are apparently absent. It includes two sub-families, the Acetabularieæ and Dasycladeæ.

Acetabularieæ.—Fertile and sterile appendages distinct. *Acetabularia mediter-*

ranea: the lower part of the long cylindrical stalk is incrusted with calcium carbonate, and fixed to its substratum by short irregularly branched rhizoids. The rhizoid-bearing portion is called the *foot*, and below it there is a thin-walled branched continuation of the stalk, called the *basal division*. Near the apex of the stalk are borne 1–4 whorls of polychotomously branched sterile appendages, which soon fall off.

Above these is an umbrella-shaped whorl of simple appendages in lateral contact, whose cavities are not shut off from that of the stalk. The whole of the upper part of the plant dies off each autumn, only the foot and basal division remaining alive through the winter. In the spring a new shoot is produced. Apparently after several years the contents of each simple appendage of the umbrella (which may now be a centimetre or more in diameter) divides up into a number of oval bodies, each surrounded by a fairly thick wall and containing chlorophyll and starch. These are the *gametangia*. After their escape by the dissolution of the umbrella, the contents of each divides up to form a number of gametes. Considerable pressure, caused by swelling of the ectoplasm and osmotic tension in the vacuole of the gametangium, bursts off a lid at one end, and the gametes escape. Conjugation only occurs between gametes derived from distinct gametangia.

Dasycladeæ.—No distinction between fertile and sterile appendages. *Dasycladus* has a single stalk-cell fixed below like *Acetabularia*, but bearing very numerous whorls of appendages, which stand so close together as to give the entire plant a resemblance to a minute fox's brush. Each appendage bears a terminal whorl of branches, and in the middle of these is a shortly-stalked, nearly spherical gametangium. The gametes conjugate, but apparently only with those from certain other plants. This fact at first led to the supposition that we had here a physiological distinction of sex in gametes, which in external appearance are all alike. This is, however, quite an unjustifiable and unnecessary assumption. We have no right to predicate sexual differences between gametes which do not show any of the well-recognized characters of male and female reproductive cells. The tendency to avoid pairing with closely related gametes, which we may call *exogamy*, is quite a distinct phenomenon, not only among isogamous Algæ, but also among many of the higher plants, where it coexists with strongly-marked sex. The phenomena of self-sterility is an extreme case of this.

Neomeris and *Cymopolia* are two tropical and subtropical genera, whose thallus is very strongly incrusted with calcium carbonate. The arrangement of the branches resembles that found in *Dasycladus*, but on the ends of the younger ones hairs are borne, which serve to protect the growing apex of the plant. In *Cymopolia*, of which the main stalk branches, and the thallus attains a considerable size, these hairs are borne by simple branches produced on special constricted and uncalcified zones of the stalk. The apices of the secondary branches are in both genera swollen up, and in close lateral contact, thus forming a continuous surface on the exterior of the plant. The calcium carbonate is deposited as a thick layer underneath these swollen ends.

A whole series of fossil forms from the chalk and tertiary deposits serve to connect the various existing types of these and allied genera.

Alliance VIII.—Confervoideæ.

The Algæ included under this alliance possess a type of thallus composed of distinct and separate cells. These cells are united usually into linear series, which form branched or unbranched threads. In a few families, however, cell-division takes place in two, or even three, dimensions, resembling some Protococcoideæ in the formation of cell-surfaces or cell-masses. Zoospores are produced by nearly all confervoid forms. Aplanospores and akinetes are common. The gametes may be isogamous, or they may show marked sexual differentiation.

Families: *Ulvaceæ, Ulotrichaceæ, Cylindrocapsaceæ, Œdogoniaceæ, Cladophoraceæ, Gomontiaceæ, Sphæropleaceæ, Chætophoraceæ, Trentepohliaceæ, Mycoideaceæ, Coleochætaceæ.*

Ulvaceæ.—This family is usually regarded as the lowest of the confervoid series. It is characterized especially by forming cell-surfaces instead of filaments. Zoospores with four flagella and isogametes with two, as well as akinetes, are formed in the group. *Monostroma* very much resembles *Tetraspora* among the Protococcoideæ, from which we may suppose the confervoid forms to have arisen in evolution. The thallus consists of a single layer of roundish or angular cells. In germination, the zygote divides to form a small hollow sphere, which splits, and extends itself to form a flat plate. At first fixed by rhizoids, the thallus later floats freely in the water. The chromatophore is a parietal plate, covering more or less of the cell-wall, and contains a single pyrenoid. Gametes (which may develop without conjugation), or zoospores may be formed in almost any cell of the thallus.

Ulva differs from *Monostroma* in possessing a thallus of two layers of cells, those of each layer dividing independently of the other. The zygote germinates to form a fixed cell thread, which later on produces the two-layered thallus. *Ulva latissima* (the Green Laver or Sea-lettuce) is very common on the rocks of our coasts near high-tide mark. It forms large green wavy fronds firmly fixed to the substratum. It is sometimes used as an article of food.

Enteromorpha is a large genus, several species of which are common on our coasts, and some in fresh water. The thallus forms a branched hollow tube, the wall of which is one cell thick. Any cell of the thallus may act as the apical cell of a branch. The apex of the branch is solid, but the cells soon round themselves off to form the wall of the tube. The gametes and zoospores resemble those of *Monostroma* and *Ulva*.

Letterstedtia is a Cape and Australian form much like *Ulva*, but with a deeply-lobed thallus. Zoospores are produced only in the cells of the lobes.

Ulotrichaceæ.—This family contains several genera common in fresh water, and some marine forms. The thallus consists of an unbranched filament of cells seldom much longer than they are broad. The chromatophore is single, parietal, and of

very various form. Zoospores are formed in most genera. Gametes, where known, are motile and isogamous. Aplanospores and akinetes are very commonly formed, under unfavourable conditions.

Ulothrix (fig. 371), the best-known genus, possesses cells of very variable length. The chromatophore, which contains several pyrenoids, is an interrupted cylinder, and may or may not occupy the whole length of the cell. When the conditions are suddenly changed, zoospores or gametes are very readily formed, the former 1–4 the latter 4–32 in a cell. According to the size of the mother-cell and the number of divisions taking place, the size of the zoospores and gametes varies greatly, the

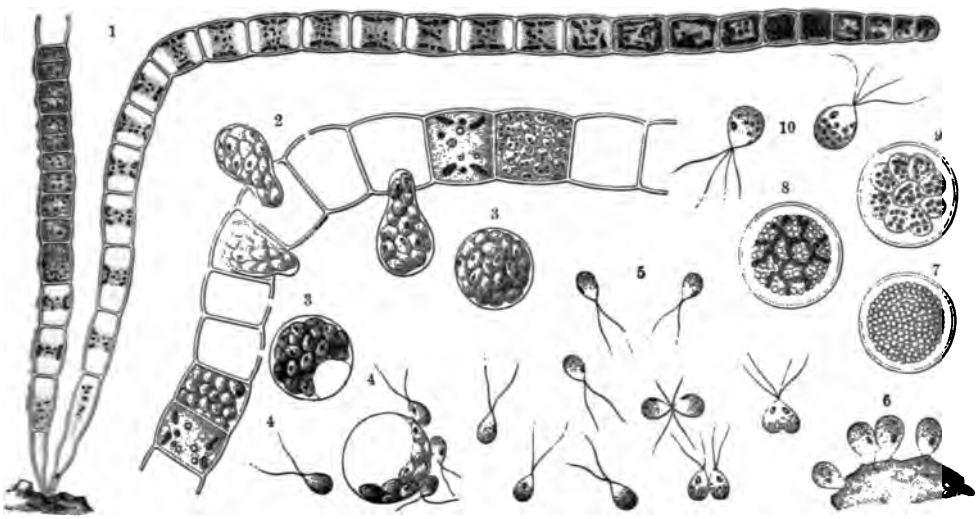


Fig. 371.—*Ulothrix zonata.*

[1] Two filaments of this plant. [2] Escape of gametes in packets. [3] Spherical packet of gametes free from the filament. [4] Separation of the gametes. [5] Gametes swimming about and pairing. [6] Products of pairing of gametes (zygotes) attached to substratum. [7–9] Zygote giving rise to zoospores. [10] Two zoospores. [1] × 250; [2–10] × 400. (Partly after Dodel-Port.)

only constant distinction between them being the number of flagella, which in the zoospores are four, in the gametes two (*cf.* figs. 371[10] and 371[5]). The zoospores or gametes escape from the mother-cell through a hole in the wall. They are surrounded by a bladder derived, probably, from ectoplasm. The swelling of this in the water helps to drag them out of the cell-cavity. The tension of the vacuole of the mother-cell, which is visible among the zoospores or gametes as a smaller bladder, also assists in pressing out the mass (figs. 371[2, 3, 4]). The zoospore settles on some solid object, and, after putting out a short root-process from its colourless anterior end, produces a new cell-thread. Some of the gametes develop parthenogenetically, in which case they germinate just like zoospores, but produce usually smaller and weaker plants. The gametes which conjugate (see figs. 371[5] and 371[6]) produce zygotes which sink to the bottom of the water, and after a period of rest grow into unicellular plants, each of which forms 2–14 zoospores (figs. 371[6, 7, 8, 9]). These probably give rise to ordinary plants.

The asexual generations of *Ulothrix* are produced during the autumn and winter, gametes being formed in spring, and the zygote resting through the summer. This course of events differs from that obtaining in most Algæ with a similar life-history. *Ulothrix* seems especially adapted to life in cold water.

Hormidium is a genus whose members grow largely on damp earth, tree trunks, &c. The chromatophore is solid, with radiating processes and a central pyrenoid. The cells of some species divide longitudinally, so as to form threads two cells broad.

Various other genera are common in fresh water.

Cylindrocapsaceæ.—Cylindrocapsa forms unbranched threads of short cells with very thick walls, each thread being fixed in the young state by a cellulose foot. The gametes show a considerable sexual differentiation. The males are pear-shaped, elongated, yellow, with two flagella at the anterior end. They are produced two in an antheridium, which is formed by the division of an ordinary cell into two or four. The protoplasm of an ordinary cell rounds itself off directly to become an egg, the wall swelling and bursting at one side to allow of the entrance of the spermatozoids. Parthenogenesis also occurs.

Œdogoniaceæ.—Œdogonium has a thallus consisting of an unbranched thread, of rather long cells, of which the basal one is fixed to some solid object. The chromatophore often forms a continuous parietal layer containing several pyrenoids. All the cells, except the basal one, are capable of division. When division is going to occur a rim of cellulose is formed inside the cell close to the upper transverse wall. After the nucleus has divided, and the new transverse wall is formed, the rim is opened, as it were, by a circular cut from without, and the tension of the cell causes a pulling-out of the substance of the rim. The result is the intercalation of a new cylindrical piece of cell-wall in the upper daughter-cell. The young transverse wall now moves up to the lower edge of the intercalated piece of membrane. The latter soon acquires the ordinary thickness of a side wall, but the segment of the old cell-wall above the spot at which the rim was formed remains projecting beyond the new piece like the eaves of a house beyond its side walls. After the cell has divided again, another projecting piece will be left in the same way, and the series of eave-like projections so formed are a very characteristic feature of the cells of an *Œdogonium*-thread. The zoospores of *Œdogonium* are formed singly in the cells of a thread. The entire cell-body, with the exception of the ectoplasm, rounds itself off and escapes from the cell by a split in the wall. An anterior circlet of cilia surrounds the colourless "mouth place," of the zoospore. In germination, the zoospore fixes itself by the mouth place, sending out short fixing processes, puts on a cell-membrane, and then grows out to form a new thread.

The gametes of *Œdogonium* are sexually differentiated.

The oogonium is formed by the swelling-up of the uppermost daughter-cell after a division. The contents round off to form a single large oosphere. Either a round hole appears in the wall, or a circular split is formed at the upper end of the oogonium, the part of the filament above rotating through a few degrees so as to

leave an opening. A certain amount of the protoplasm of the oosphere is extruded at this spot, and forms a sort of canal of mucilage, through which a spermatozoid passes in fertilization. The spermatozoids are produced one or two in an antheridium, which are short cells poor in chlorophyll, formed by the repeated division of certain cells of a thread. The spermatozoids resemble small zoospores. In some cases they are not produced directly from the cells of a thread, but the latter give rise to special zoospores called *androspores*, which escape and settle either on or in the immediate neighbourhood of an oogonium. The androspore then germinates, producing a small structure called a *dwarf male*. This consists of a very few cells, one or more of which become antheridia, and opening by a lid, gives rise to spermatozoids, one of which pierces the canal of the oogonium, and fuses with the oosphere. The oospore, which is of a red or brown colour, produces four zoospores in germination.

Bulbochæte is a genus resembling *Œdogonium* in its life-history, but consists of a branched thread, only the basal cell being capable of dividing. The cells bear characteristic hairs, swollen at the base, whence the name of the genus.

Species of *Œdogonium* and *Bulbochæte*, which are both genera of considerable size, are found in our ponds and ditches.

The next three families are distinguished from all other *Confervoideæ* by possessing more than one nucleus in each cell.

Cladophoraceæ.—Cladophora is a very widely distributed genus, inhabiting both fresh and salt water. A great number of species have been described, but it is doubtful whether many of the forms are entitled to specific rank.

The thallus has a very characteristic habit. It is fixed below by an elongated basal cell, and is profusely branched, sometimes forming a spherical mass. The elongated cells possess parietal chromatophores, which cover the whole cell-wall, and possess many pyrenoids. Sometimes the chlorophyll-layer is separable into distinct angular plates. There are many nuclei in the layer of protoplasm immediately within the chlorophyll.

Many zoospores are produced in each cell. The nuclei divide a good deal, the pyrenoids disappear, and the protoplasm then divides into a number of separate masses, each of which forms a single zoospore with either four or two flagella. Gametes with two flagella are formed in many species quite like the zoospores. The zygote germinates directly to form a new *Cladophora*-plant.

The Cladophoraceæ show on the one hand a transition to the Siphoneæ, and on the other, through certain genera with unbranched thallus and few nuclei in each cell, to the Ulotrichaceæ.

Gomontiaceæ.—Gomontia polyrhiza is an isolated form which perforates the shells of various marine molluscs, such as the whelk, the oyster, the mussel, &c. The thallus radiates on the surface of the shell, and sends branches into the substance, gradually disintegrating it. Certain branches become zoosporangia or aplanosporangia; these lose their attachment to the thallus and form fresh rhizoids. The zoospores are pear-shaped, and germinate directly to form a new thallus.

Sphæropleaceæ.—*Sphæroplea annulina* is a curious Alga which appears occasionally on flooded fields or in other situations. Its thallus consists of simple threads of cells which are of very various length, sometimes enormously long. The side walls are thin, but the transverse walls are often thick, and both are liable to have curious thick and quite irregular projections of cellulose. The chromatophores form irregular rings at intervals, and contain many pyrenoids. There are many nuclei, and several variable vacuoles in each cell. All the cells may produce sexual organs, the threads being either monœcious or dicœcious. The contents of the cells which become antheridia become yellow-red, and break up to form a great number of elongated, pointed spermatozoids. These escape through small holes in the wall. In the oogonia the protoplasm divides to form one or two series of spherical oospheres, each with a colourless spot. The oospore has three membranes, of which the outermost is folded so as to give the oospore a star-like appearance.

In germination the oospore produces 1–8 zoospores, which have a green posterior and a pale-red anterior end. Each eventually stretches itself to form a spindle-shaped cell, and a multiplication of nuclei and pyrenoids takes place before transverse divisions occur and a new *Sphæroplea*-filament is produced. Parthenogenesis occurs, but apparently no zoospores are formed other than those produced in the germination of the oospore.

Chætophoraceæ.—This family contains forms with a branching thallus, the branches often ending in fine hairs. The chromatophore is parietal, with one or more pyrenoids. Zoospores with two or four, and gametes with two flagella are produced.

Stigeoclonium, *Draparnaldia*, and *Chætophora* are three genera common in fresh-water in this country, and all very slimy to the touch. In the first-named genus the thallus is fixed by means of a basal disc of cells, the *sole*; the branching is simple and irregular, the branches often ending in long multicellular hairs. *Draparnaldia* shows a marked distinction between axis and appendages. The axial cells are much larger, and at the same time poorer in chlorophyll than those of the branches. The branches come off in bunches, and often end in many-celled hairs. The chromatophore possesses many pyrenoids varying in number according to the size of the cell. *Chætophora* possesses a thallus whose threads radiate and branch in all directions. The whole is surrounded by a mucilaginous investment of considerable firmness, sometimes almost leathery in consistence, so that a *Chætophora*-plant has the appearance of a slimy green ball.

There are several other genera belonging to this family, many of them being epiphytic or endophytic. *Entoderma* lives in the cell-membranes of the Brown Sea-weed *Ectocarpus*.

Trentepohliaceæ.—This family differs from the last in possessing no hairs, and in forming its zoospores in special zoosporangia.

Trentepohlia is a fairly large genus containing forms mostly living in the air on damp stones and similar situations. The thallus consists of rounded thick-walled cells, and is dichotomously or irregularly branched, partly creeping, partly upright.

The chromatophores are many, disc-like, and angular, with no pyrenoids. The cell-contents is usually much marked with hæmatochrome. The zoosporangia and gametangia are usually terminal, often swollen cells. The gametes and zoospores are much alike. *Trentepohlia Iolithus*, growing on damp stones, is known as the "Violet-stone" from possessing a scent which recalls that of violets. *T. umbrina* is often attacked by lichen-forming Fungi. *T. spongophila* inhabits the jelly of *Ephydatia* (*Spongilla*) *fluviatilis* in a certain volcanic lake in Sumatra. The situation is very advantageous to the Alga, but the Sponge seems to suffer from the piercing of its tissue by the guest. *Trichophilus* is a nearly allied form which lives in the hollow hairs of the Three-Toed Sloth.

Mycoideaceæ.—These are epiphytic or parasitic forms nearly allied to the two preceding families, and probably derived from one of them. They form regular discs of cells often attached to the host by much-branched unicellular rhizoids. The disc grows by regular divisions of its marginal cells. Zoospores and sometimes gametes are formed in all or some of the cells.

Chætopeltis forms very regular discs of cells on fresh-water plants in Europe.

Mycoidea (*Mycoidea parasitica*) forms discs of cells between the cuticle and epidermal cells of Camellias, Rhododendrons, &c. in the East Indies and South America. In this position it withdraws a good deal of water from the tissue of the leaf, and this leads to the dying of the leaf-cells in a gradually increasing area round the parasite. Eventually a hole is formed right through the leaf, and the *Mycoidea*-thallus occupying a position all round the area of dead tissue continues to increase. Zoospores are only formed in the wet season, at which time alone have they any chance of swarming and germinating on the surface of the leaf. In this position primary (embryonic) discs are formed, many of which die, and others are attacked by Fungi to form Lichens, but some succeed in sending processes through the cuticle and establishing themselves below.

Coleochætaceæ.—This family contains a single small genus, *Coleochæte*, which forms radiating, dichotomously branching rows of cells, usually on the surface of other plants in fresh-water. If the cell-rows are in lateral contact, a close disc is formed (*C. scutata*), if separate a looser one (*C. soluta*), or the branching may be rather irregular (*C. divergens*). The chromatophore is parietal and disc-shaped, and contains a single pyrenoid.

Zoospores can be produced in all or only the end cells of the rows. A single one is formed from each cell. In germination a new plant is directly formed.

Coleochæte is oogamous, the plants being either monœcious or dicœcious. The oogonium is always formed from the end cell of a row. The cell swells and puts out a narrow tube which opens at the end, and extrudes a drop of mucilage. The protoplasm of the swollen basal part then rounds itself off. In the forms with a disc-shaped thallus, the antheridia are produced by the division into four of the members of certain cell-groups. Each daughter-cell (antheridium) then liberates a single spermatozoid. In the branching forms certain end cells form flask-shaped swellings (antheridia), which are cut off from the mother-cell by transverse walls.

Each antheridium then liberates a spermatozoid. Fertilization has not been observed, but there can be no doubt that a spermatozoid passes down the neck of the oogonium and fuses with the oosphere. Subsequently the neck of the oogonium breaks off, the oospore puts on a cell-wall, and the neighbouring cells branch so as to form a closely investing cortex of cells round the oospore. The contents of these cortical cells turn red-brown; and after a resting stage the cortex comes off, the oospore having in the meanwhile divided to form a disc of cells, each of which gives rise to a zoospore, which escapes and germinates to form a new plant.

The structure of the oogonium, and the formation of a cortex round the oospore, as well as the formation of "carpospores" by the latter, recall the simpler Red Sea-weeds, a group which some authorities consider to be derived from some form like *Coleochæte*.

The indirect formation of new plants by the products of division of the zygote, a phenomenon we have already met with in *Pandorina*, *Hydrodictyon*, *Ulothrix*, *Œdogonium*, and other forms, is probably the means by which the sporophyte generation of Mosses and Liverworts arose. At first the zygote gave rise at once to spores, but later on a certain amount of sterile tissue was produced in addition, and this formed the body of the sporophyte.

Alliance IX.—Conjugatæ.

Families: *Desmidioideæ*, *Spirogyraceæ*, *Zygnemaceæ*, *Mougeotiaceæ*.

This is a very sharply characterized alliance of Green Algæ. It is indeed difficult to determine its affinities. The forms belonging to it are especially characterized by never forming zoospores, and by possessing *aplanogametes*, *i.e.* gametes which, instead of escaping from the mother-cell and swarming freely, never leave the cavities of the cells in which they are produced. When conjugation is about to occur the two cells (gametangia), the contents of which will form gametes, approach one another, and their walls come into contact, either directly, or by the putting out from one or both cells of a short cellulose tube. The area of wall at the place of contact breaks down, and the whole or part of the contents of each cell then fuses with the corresponding protoplasm of the other to form a zygote.

The chromatophores of the Conjugatæ, though very various in the different families, are all very different from the types met with among the other Green Algæ.

I. *Desmidioideæ*. Cell-contents and outline symmetrically arranged on each side of a given median plane which is often coincident with a more or less deep constriction. Often unicellular.

II. *Zygnemoideæ*. Cells cylindrical, without median constriction, always forming threads.

1. *Spirogyraceæ*. Chromatophores one or more, parietal, spiral.
2. *Zygnemaceæ*. Chromatophores two, axile, roundish.
3. *Mougeotiaceæ*. Chromatophore single, axile, plate-like.

Desmidioideæ.—The Desmids are a large family of fresh-water forms numbering over a thousand species. Perhaps their most favourite habitat in this country is the water which collects and stands between mosses and similar plants on impervious soils. Many of the Desmids are among the most beautiful of algal forms.

The great characteristic of the Desmid-cell is its almost invariable division into two symmetrical halves, often separated by a circular constriction (*cf.* fig. 372). The cell-membrane usually consists in fact of two distinct valves whose edges meet in this median plane. In cell-division these two valves are forced apart, a new cylindrical piece of membrane being intercalated between them. A transverse wall

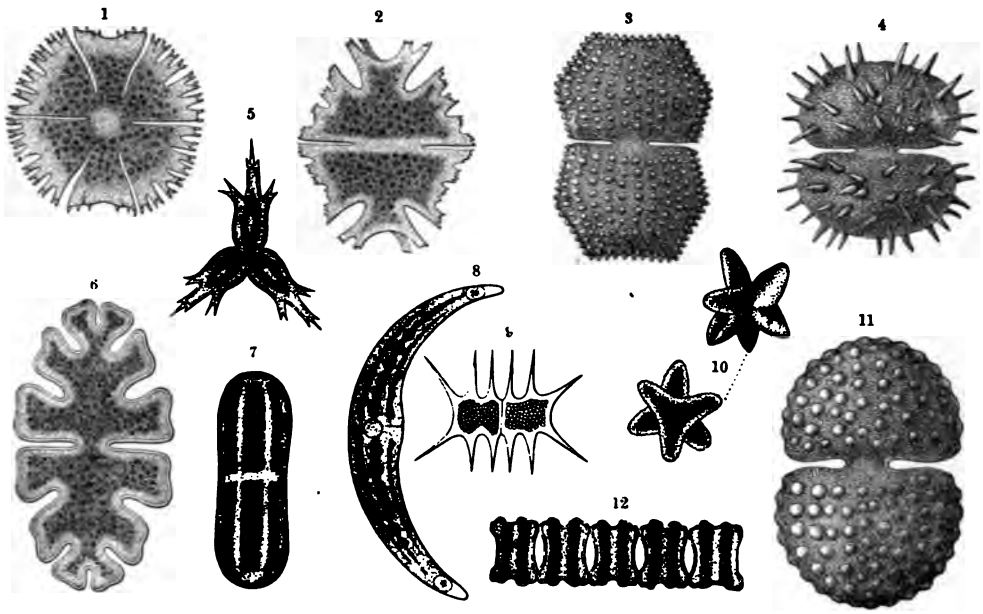


Fig. 372. Desmids.

[1] *Micrasterias papillifera.* [2] *Micrasterias morsa.* [3] *Cosmarium polygonum.* [4] *Xanthidium aculeatum.* [5] *Staurastrum furcatum.* [6] *Euastrum oblongum.* [7] *Penium Brebissonii.* [8] *Closterium Lunula.* [9] *Xanthidium octocorne.* [10] *Staurastrum alternans* (two views). [11] *Cosmarium tetraophthalmum.* [12] *Aptogonum Desmidium.* All the figures magnified about 200 times.

is then formed at the equator, and each half of the new piece of wall gradually assumes the characters of the old half-cell to which it belongs.

The actual form of the cell is very various; it is often lobed, and its wall sculptured in various ways. A good idea of the shapes of some of the commoner types can be obtained by an inspection of fig. 372; see also fig. 25A, *i*, *k*.

The chromatophores are also extremely various in form. A common type is an axile rod bearing longitudinal plates which radiate in all directions. Each chromatophore contains one or more pyrenoids.

The cell-membrane is usually perforated by series of regularly arranged, very minute pores which give exit to extremely delicate filaments of protoplasm. The projecting end of each filament is surrounded by a mass of mucilage, and these masses together form a complete sheath covering the entire cell, and sometimes even

groups of cells (*cf.* similar phenomenon in Diatoms, p. 626). Many Desmids possess the power of locomotion. Their movement is slow and creeping, and although the means by which it is brought about are by no means fully understood, it has been shown to have a connection with the excretion of mucilage, and to stand in relation with light and gravitation. Some forms (e.g. *Closterium* and *Penium*, figs. 372[8] and 372[7]) have a curious rotating movement, one end being temporarily fixed while the other moves up towards the source of light.

Conjugation takes place as already described, the conjugating cells either coming into direct contact, or putting out short tubes. The conjoined tubes are known as the *conjugation-canal*. The zygote may be formed either in this or in one of the conjugating cells. The membrane of the zygote consists of three layers, the outer one being sculptured in various ways. In germination, the outer, sculptured membrane is burst open, and the protoplasm divides to form 2–8 cells which gradually take on the characters of the adult individual.

The cells of the thread-forming Desmids (*cf.* fig. 372[12]) possess all the characters of the unicellular types, the daughter cells simply remaining together after division (which always occurs in one plane) has taken place.

Spirogyraceæ.—This family contains the single genus *Spirogyra*, many species of which are amongst the commonest Algæ in our ponds and ditches. They form green or yellowish-green slimy masses on the mud at the bottom or floating at the surface of the water. Such a *Spirogyra*-mass usually contains several species, although the bulk of it is often formed by one.

The cells of the different species vary much in diameter, from the delicate *S. tenuissima* which is only about one hundredth of a millimetre across, to *S. crassa*, which forms coarse threads as much as one seventh of a millimetre thick. Roughly speaking, the broader the cell, the greater number of chromatophores it possesses The smaller species possess only one spiral band in each cell (fig. 25A, *l*), the largest as many as eight or nine.

Each *Spirogyra*-cell is a cylinder, in most cases considerably longer than it is broad (though the relation of length to breadth is variable even in one and the same species), with a very delicate layer of protoplasm lining the wall, and a large central vacuole. Each chromatophore forms a band embedded in the protoplasm, and twisting spirally round and round the cell at an approximately constant angle. When there are more bands than one they cross each other at regular intervals, forming a beautiful lattice-work. In some species each band makes several complete turns in its course down the cell (fig. 373); in others, it may be inclined at such a small angle with the long axis that it makes less than a complete turn in the length of the cell. In *S. orthospira* the bands are practically parallel with the long axis, so that they do not follow a spiral course at all, but form straight bands. Each chromatophore may be isodiametric, or, on the other hand, it may form a flattened band. In the latter case its edges are usually irregularly scalloped. A single row of pyrenoids at larger or smaller intervals is found in each chromatophore.

Each cell contains a single nucleus which occupies approximately the centre of the cell. In the larger species it is suspended in the middle of the vacuole by a number of branching threads, many of which run into the peripheral protoplasm opposite a pyrenoid. This can be particularly well seen in the large *S. crassa*. It suggests that the nucleus plays some active part in the function of starch formation. In the smaller species when the breadth of the cell is perhaps not more than double the diameter of the nucleus, the latter often lies in the concavity of, and in contact with, a chromatophore. In this case the protoplasmic threads are not so obvious.

All the cells of a *Spirogyra*-thread are capable of division. After the nucleus has divided, a rim of cellulose is secreted in the equatorial plane of the cell. This is gradually added to from within, till a complete disc of cellulose is formed, separating the two daughter-cells. Curious folds are always formed on the transverse walls of some species. Each fold forms a circular rim near the periphery of the transverse wall and projecting into the cell cavity. These folds are sometimes completely evaginated, the transverse wall thus having its surface considerably increased and becoming strongly concave towards the cell-cavity. This happens especially when two cells are separating from one another, or, when a gamete is formed from a neighbouring cell.

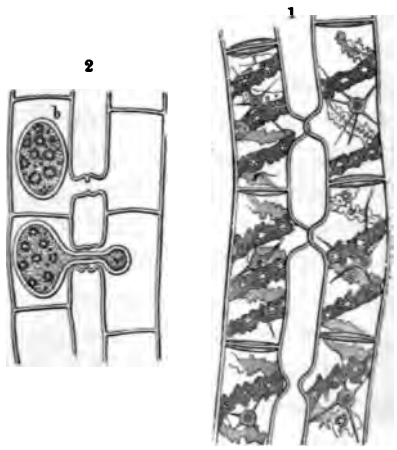


Fig. 373.—*Spirogyra*.
[1] Two filaments commencing to conjugate.
[2] Formation of zygotes.

Multiplication is often effected by the breaking up of a filament into segments consisting of a few cells each which go on dividing and form a new thread.

Conjugation takes place in two ways; a zygote being produced either from gametes formed in two neighbouring cells of the same filament, or in two cells belonging to distinct filaments. In the former case a small swelling is formed opposite a septum, a small area of the septum breaks down, and the contents of one cell, rounding itself off from the walls, passes through the aperture thus formed and fuses with the contents of the other cell, also rounded off, to form a zygote, which immediately puts on a membrane, and enters upon a resting stage.

In the second or "ladder-type" of conjugation (fig. 373, and fig. 25A, *l*), two filaments come to lie side by side, and the contents of some or all of the cells of one thread round off, each cell-wall growing out into a short tube towards a cell of the other thread. Each cell of the other thread then either swells up towards this tube or puts out a similar tube, and the walls coming into contact are absorbed, an open canal (conjugation-canal) thus being formed between the two cells. The contents of the first cell then passes through the canal into the cavity of the second, the contents of which has also rounded off, and fusion occurs between the two gametes. The whole of the cells of two filaments frequently conjugate about the

same time, and the series of conjugation-canals thus formed give the appearance of the rungs of a ladder. All the zygotes are formed in one filament, which we may consider as physiologically female, its gametes being relatively passive compared with those of the other (male), which initiate the process, and actively pass through the canals. The relative behaviour of the two threads shows that an influence is exerted by the male on the female cell, the former determining the outgrowth and direction of the tube belonging to the latter, as well as the rounding off of the female gamete. If the female tube is not put out opposite the male, the former bends round to meet the latter, and if the male cell dies in the middle of the process, the female tube goes on growing indefinitely, and the female gamete does not round itself off. The influence exerted is in all probability a chemical influence, a phenomenon which seems to occur in connection with the process of the conjugation of gametes throughout the vegetable kingdom (*cf.* the remarks on pp. 68 and 413).

The chromatophore of the germinating zygote is formed from that of the female gamete alone, the band belonging to the male gamete gradually disintegrating in the zygote. This is an interesting example of the reduction of the specially vegetative portion of the male cell.

Zygnemaceæ.—The cell of *Zygnema* differs from that of *Spirogyra* (fig. 25A, m) in its remarkable and beautiful star-shaped chromatophores. There are two of these in each cell, occupying positions equidistant from the centre of the cell. Each possesses a rounded central portion, containing a single pyrenoid, from which thicker or thinner processes radiate in all directions. The nucleus forms a bridge between the two chromatophores.

Conjugation takes place much as in *Spirogyra*, the zygote being formed either in the conjugation-canal or in one of the conjugating cells.

Mougeotiaceæ.—This family is characterized by the possession of single axile plate-like chromatophores, and by the fact that part of the protoplasm of a conjugating cell does not enter into the formation of the zygote.

The chromatophore, which possesses a single row of pyrenoids, can alter its position according to the strength of the light to which it is exposed. In moderate light the plane of its surface is at right angles to the line of the incident rays, in stronger light it places itself in the same plane as these rays, so that they only fall upon its edge. In very strong light it contracts to form an irregular body in the centre of the cell.

In conjugation the cells of two threads either put out tubes, and form spherical zygotes in the conjugation-canals (*Mesocarpus*-type), or the two cells bend towards one another, and form a four-sided zygote, one side of which occupies the centre of each cell. The wall of the zygote thus cuts off the two ends of the two cell cavities, so that the zygote appears as if it were surrounded by four empty cells (*Staurospermum*-type). These, however, soon break off.

Gonatonema forms so-called aplanospores in the following way. A cell increases to double its former length, its contents (chromatophore, &c.) dividing into two parts. A swelling is formed in the middle of the cell, into which the two chromato-

phores and the bulk of the protoplasm move from each end. A wall is now formed round the contents of this swelling. Although the behaviour of the nucleus has not been followed, this certainly suggests a reduced process of conjugation, each half of the cell representing a gamete.

Mougeotiopsis is a genus whose chromatophore possesses no pyrenoids.

Alliance X.—Charales.

Family: *Characeæ*, the Stoneworts.

Are green submerged plants with segmented axes bearing whorls of leaf-like appendages at the nodes, upon which the antheridia and oogonia are borne. The antheridia are spherical and contain a large number of filaments, each cell of which produces a spermatozoid with two long cilia. The oogonium consists of an egg-cell inclosed in five spirally-twisted, tubular cells; on germination the egg-cell gives rise to a simple segmented filament (the pro-embryo) from which the adult form arises as a lateral bud. There are no swarm-spores. Vegetative propagation is by bulbils, detached branches, &c. This alliance, though placed here in sequence with the other alliances of Green Algæ, is probably remote from them in actual affinity. The Charales form an isolated and anomalous group, and various views are entertained as to their true position.

Members of this group occur very commonly in ditches, ponds, &c., and in brackish water. In the Norfolk Broads very extensive growths of these plants occur in the muddy bottom of the Broads, the living plants resting on the decomposing remnants of former generations; in this way the bottom level is being gradually raised.

Chara fragilis (see fig. 374) is perhaps the commonest species of the group, and is cosmopolitan in its distribution. The plant is some 12 inches high, and consists of axis with whorled leaf-like appendages inserted at the nodes. The axis consists of a number of long cells (the internodal cells) with which alternate the short nodal cells. The former remain undivided, whilst the latter originate the appendages and also a number of tubes, which, growing both upwards and downwards, everywhere cover in the internodal cells, forming a sort of cortex. The "leaves" have a structure essentially similar to that of the stem; they are, however, of limited growth (fig. 374[3]). They bear at their nodes tiny leaflets and the reproductive organs. The oogonia and antheridia occur together in this species (figs. 374[2] and 374[3]), the latter below the former. The antheridia are spherical orange-coloured bodies, consisting of eight shields or plates whose edges dovetail into one another; each bears a process (the manubrium) on its inner surface, and each of these manubria bears a tuft of filaments (fig. 374[5]), in every cell of which a coiled spermatozoid is produced bearing 2 long cilia at the tip (figs. 374[6] and 374[7]). The shields now disarticulate and the spermatozoids escape. The oogonia (or amphigonia) remotely resemble the archegonia of Ferns (*cf.* fig. 346[2], p. 472). Each contains a big oval egg-cell inclosed in a sheath of 5 tubes spirally wound around it. The tips of these tubes

form a crown surmounting the oogonium (fig. 374[8]). At fertilization the spermatozoids penetrate between the cells of the crown, so reaching the egg-cell. The whole oogonium is soon detached and remains dormant through the winter. In the spring it germinates, pushing out a tube which becomes transversely segmented. This is the pro-embryo. From it, as a lateral bud, the adult sexual plant arises. This process resembles that of the Mosses, in which the leafy Moss-plant arises from

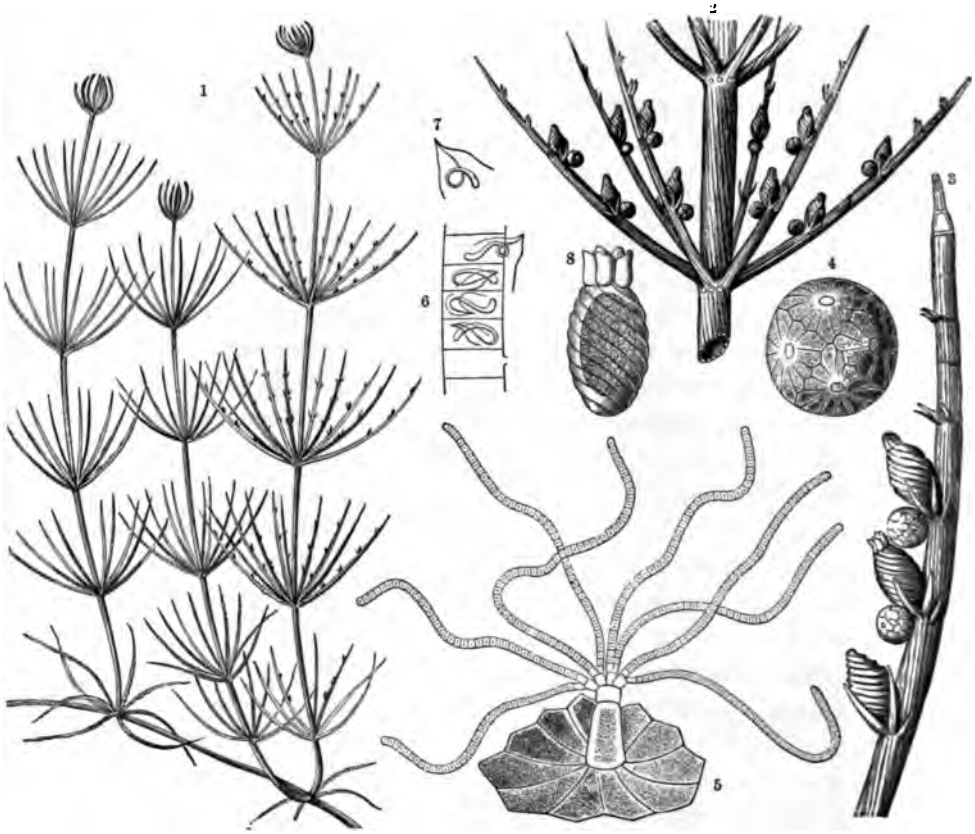


Fig. 374.—Structure and reproduction of *Chara fragilis*.

[1] A portion of the plant. [2] A piece of the axis with appendages, upon which are inserted the sexual organs. [3] A single appendage, showing the flask-shaped archegonia and spherical antheridia. [4] A single antheridium. [5] A plate of an antheridium with manubrium and whip-like filaments of cells containing spermatozoids. [6] Several cells from one of the whip-like filaments: the cells in the middle contain each a spermatozoid; the spermatozoid is escaping from the uppermost cell; the lowest cell is already vacated. [7] A single spermatozoid. [8] Archegonium inclosing the egg-cell. [1] nat. size; [2] ×10; [3] ×15; [4] ×35; [5] ×100; [6] ×300; [7] ×500; [8] ×50.

the protonema as a lateral bud. But the comparison with Mosses must not be pushed too far, as in *Chara* there is no sporogonium. There are some 67 species of *Chara*, of which *C. fœtida* is also very common. Many of them are covered with stiff hairs, and they are for the most part brittle owing to the incrustation of carbonate of lime (*cf.* vol. i. p. 260). The phenomenon of parthenogenesis in *Chara crinita* has already been described in detail (pp. 463, 464).

In *Chara stelligera* (= *Tolypellopsis ulvoides*) the nodes of the stem become

swelled out with starch, and assume a stellate form (starch-stars). They serve as organs of vegetative propagation.

The other large genus of Characeæ is *Nitella*. It is especially distinguished by the fact of its stems and leaves being destitute of cortex. There are 67 species of *Chara* and 77 of *Nitella*.

Characeous fruits (*Gyrogonites*) are met with in large numbers in the lower chalk and in tertiary formations. Only rarely are fragments of the stems, &c., recognized.

Alliance XI.—Phæophyceæ.

Families: *Ectocarpaceæ, Sphacilariaceæ, Cutleriaceæ, Laminariaceæ, Fucaceæ.*

Includes the whole series of the Brown Sea-weeds, essentially characterized by the fact that their chlorophyll-corpuscles include, in addition to chlorophyll, a brown pigment, Phycophæin, which masks the green colour of the chlorophyll. The forms included under this alliance are all multicellular, and range from simple threads of cells to large complex forms showing a differentiation into a root-like attachment-organ, stipe, and expanded leaf-like frond. In several of these larger forms the internal structure almost rivals that of Flowering Plants in complexity. Within the limits of the group we find sexual reproduction, in some cases by the fusion of equivalent motile gametes (*cf.* p. 50), in others of well-marked egg-cells or spermatozoids. Fertilization and the complete life-history has been studied in relatively few cases.

Ectocarpaceæ.—These are mostly filamentous and often branched. Attached to the branches are the sporangia and gametangia. From the former motile zoospores are liberated. From the latter similar bodies—the gametes—are liberated. These possess two cilia, attached *laterally* to the gametes. The process of fertilization has been followed in *Ectocarpus siliculosus*. Certain of the gametes come to rest first, and these are approached by a number of other gametes, which swarm around them. Ultimately one of the swarming gametes fuses with the resting gamete and fertilizes it. This process has been thought to indicate the existence of a certain sexual differentiation amongst the gametes, the gamete which comes to rest first being the egg-cell. However, there is no demonstrable structural difference between them.

Sphacelariaceæ.—The filaments consist of many layers of cells. Reproductive organs agreeing in the main with the last-named family.

Cutleriaceæ.—Mostly branched, ribbon-like forms. The gametangia are arranged in tufts, and the gametes differ in size, but both possess two cilia.

Laminariaceæ.—Perhaps the most interesting family of the alliance. Many forms are known to liberate motile reproductive cells from various portions of their surface, but the fate of these bodies has not been ascertained. They are large marine forms, some of them attaining gigantic dimensions. *Laminaria digitata*, which grows in quantities near low-water mark on our coasts (where it forms a regular "Laminaria-zone"), has a tuft of powerful roots holding it to the rocks, a long

stipe, and a flat, expanded leaf, deeply lobed like a hand. It is often met with two metres in length. The leaf is of a leathery consistency, and the flattened or cylindrical stalk has a wide parenchymatous cortex and central "medulla", in which run curious tubes (the "trumpet hyphæ") which swell out at intervals, the swelling being traversed in a transverse direction by a delicate sieve-plate. The stem possesses a peripheral cambium-like zone, which adds each year a new zone of tissue to the cortex. The stems, which are sometimes found much thicker than one's

Fig. 375.—Laminariaceæ, with perforated fronds.

[1] *Agarum Gmelini* (after Riocreux). [2] *Thallasiophyllum clathrum* (after Postels and Ruprecht). Both much reduced.

thumb, show in section a series of rings, reminding one of the annual rings of a dicotyledonous stem. A long ribbon-like form, *L. saccharina*, is also common on our shores. In other forms the frond is branched and often curiously appendaged at the base. In the two genera represented in the accompanying illustration (figs. 375 [1] and 375 [2]) *Agarum* (from the North Atlantic) has a simple, *Thallasiophyllum* (North Pacific) a compound frond. In both the fronds are perforated or fenestrated. *Lessonia* (Southern Pacific) attains to tree-like dimensions and is much branched; it has a stem as thick as a man's thigh. But the two most impressive genera are *Macrocystis* and *Nereocystis*. The former, which occurs throughout the southern oceans and on the western coast of N. America, consists of a long stalk, sometimes attaining a length of 300 metres, but in thickness not exceeding a penholder. To

this stalk are attached a series of long ribbon-like leaves, each of which, just at its point of insertion upon the stem, swells into an air-bladder about the size of a pigeon's egg. Thus the stem, which is attached below, is buoyed up, and the long leaves depend into the water. In structure the stem is not unlike that of a *Laminaria*; but it possesses in addition to the medulla, with its trumpet hyphæ, a zone containing large sieve-tubes, which resemble those contained in the soft bast of a Flowering Plant (*cf.* vol. i. fig. 10[4], p. 45, and fig. 125[7], p. 469). *Nereocystis*, occurring on the W. coast of N. America, consists of a long stalk (attaining to a length of nearly 100 metres), attached at its lower extremity and expanding above into a huge retort-shaped air-sac, from the surface of which a number of fronds (6–10 metres in length) arise. Like *Macrocystis*, its stem contains well-marked sieve-tubes. It is used by the Aleutians as fishing-line. Of Laminariaceæ about 90 species have been distinguished (including 30 species of *Laminaria*).

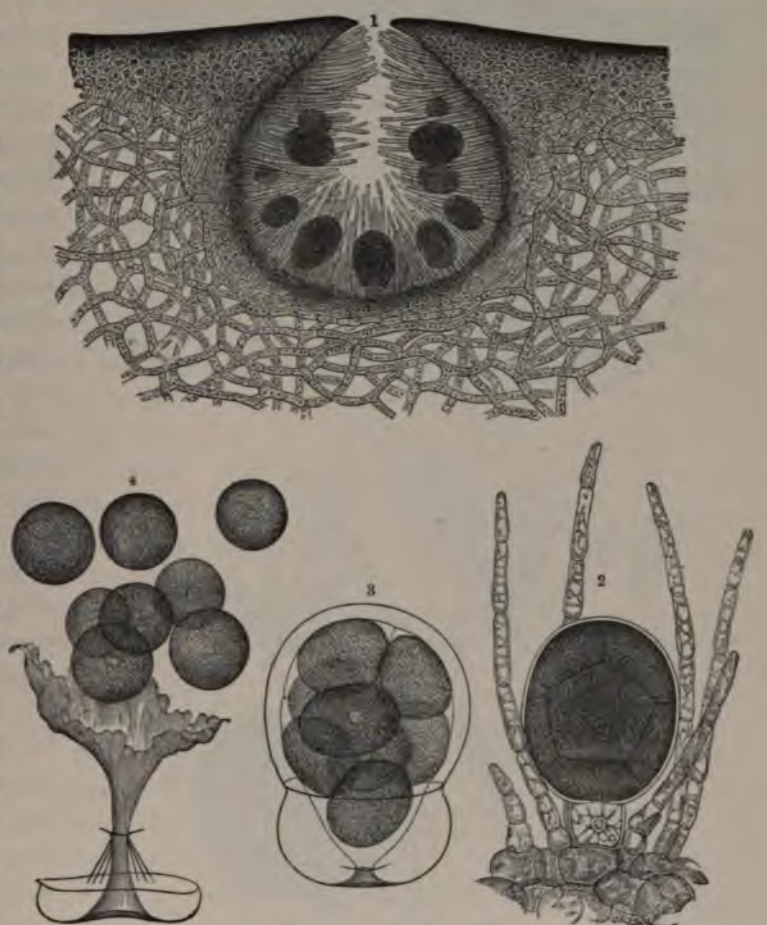


Fig. 376.—*Fucus vesiculosus.*

[1] Vertical section through a female conceptacle. [2] A single oogonium from the conceptacle surrounded by sterile hairs. [3] A detached oogonium containing 8 egg-cells; the inner lamella of the wall is much swollen. [4] Liberation of the egg-cells. [1] ×50; [2], [3], [4] ×160. (After Thuret.)

Fucaceæ.—Includes a number of the larger common sea-weeds. They are characterized—like the last family—by a segmentation into a well-marked shoot and organ of attachment. The former is usually flattened and branched, and often bears air-bladders. Reproduction is by means of spermatozoids and non-ciliated egg-cells, which arise in flask-shaped hollows (conceptacles) on definite portions of the shoot or frond. Asexual reproduction by detachment of fragments.

The Wrack-genus *Fucus* forms an exceedingly conspicuous feature of our seashore flora. The shoot is flattened and ribbon-like, branching in one plane and attached to stones, &c., by a sucker-like disc. In many species there is a midrib, as also air-bladders. The tips of many of the branches are studded with little rugosities — really indicating the presence of pear-shaped hollows, the conceptacles. From the lining of these conceptacles project the oogonia and branched filaments bearing antheridia respectively. As a rule the male and female organs occur on distinct plants, though in some species the antheridia and oogonia occur side by side in the same conceptacle. The structure of the sexual cells and the act of fertilization (which occurs outside the mouth of the conceptacle) have been fully described on pp. 51, 52; they are represented in figs. 376 and 377. Sixteen species of *Fucus* are distinguished, and they occur for the most part in the seas of the northern hemisphere. *Fucus vesiculosus* and *F. serratus* are the commonest. Several other genera are represented in Britain, *Pelvetia*, *Ascophyllum*, *Cystoseira*, *Halidrys*, and *Himanthalia*. The last-named genus is altogether peculiar, and consists of a top-shaped body attached by its pointed end, whilst from the upper surface of the "top" arise several ribbon-like outgrowths which branch repeatedly and attain to a length of several metres. It is upon these ribbons that the conceptacles are borne. Of exotic forms a few may be mentioned. *Durvillæa* from the southern seas resembles a thick, fleshy *Laminaria* in habit; from the summit of its thick stipe arise a

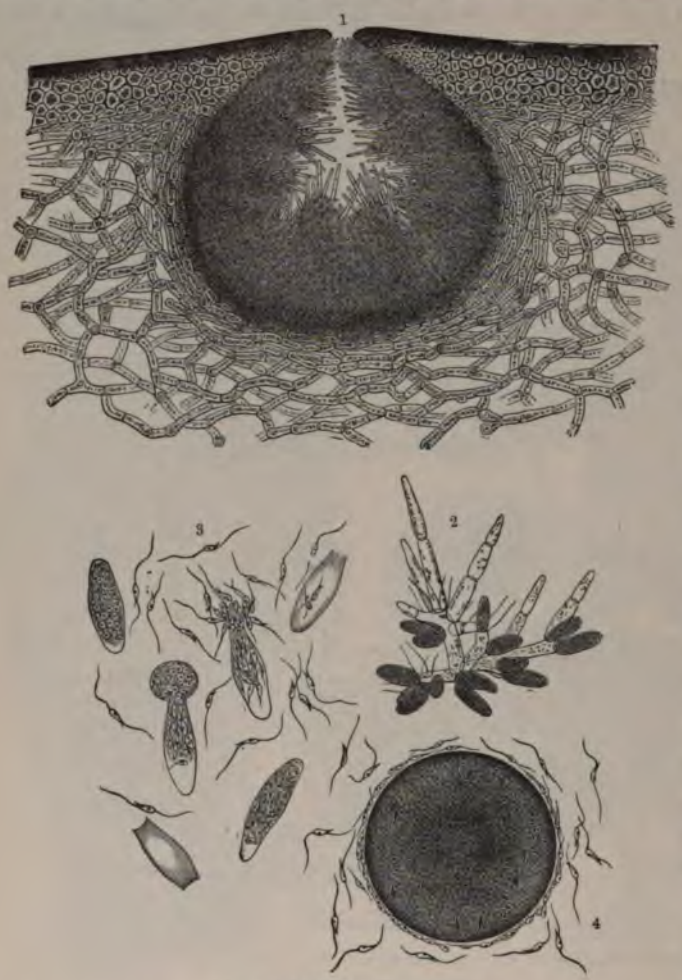


Fig. 377.—*Fucus vesiculosus.*

[1] Vertical section through a male conceptacle. [2] A portion of one of the shrubby, branched hairs bearing antheridia. [3] Spermatozoids escaping from the antheridia. [4] Spherical egg-cell with spermatozoids attached. [1] × 50; [2] × 160; [3, 4] × 350. (After Thuret.)

number of irregular fleshy lobes, which are produced into branching, whip-like filaments. Its tissues possess a curious honey-combed structure. It is stated that in Chili, &c., *D. utilis* is used as an article of food. *Sargassum* is distinguished by its high differentiation. It has cylindrical stalks bearing leaf-like appendages, and little stalked spherical air-bladders, and receptacles for the sexual organs. Some 150 species of this very varied genus are known, scattered over the warmer zones of the world. Particular interest attaches to the Gulf-weed (*Sargassum bacciferum*, fig. 378) which forms the chief component of the floating masses of Sargassum in certain regions of the Atlantic. The Sargasso Sea has received its name from the enormous amounts of this floating weed which are met with there. It occupies an area in the Atlantic perhaps equal to that of the continent of Europe. There are two main accumulations, the larger south-west of the Azores, the smaller situated between the Bermudas and Bahamas, whilst connecting them is a narrow belt. The exact nature of these accumulations is not ascertained. According to one view the Gulf-weed actually lives a pelagic life, growing and multiplying in this huge eddy in mid-ocean, and is thoroughly adapted to its special environment; whilst, on the contending hypothesis, the vegetation of the Sargasso Sea is purely ephemeral, does not reproduce, and is constantly renewed by ocean currents, which bring with them countless fragments forcibly torn by tempests from the shores of Florida and the Bahamas. It is further alleged that the floating Gulf-weed is met with only in a condition more or less unhealthy (moribund) and in various states of decomposition.

Fig. 378.—A branch of the Gulf-weed, *Sargassum bacciferum*, with leaves and air-sacs.

The weak point in the latter hypothesis is the lack of convincing evidence to show that *S. bacciferum* grows attached in the region of the West Indies, &c., in quantity sufficient to supply the Sargasso Sea. Of another species, *S. vulgare*, there is plenty, but this is not the prominent constituent of the Sargasso Sea—indeed a trained algologist, in passing recently through this sea, examined samples amounting to more than a ton, but it was only *S. bacciferum* he found. Here, evidently, is still matter for the leisured naturalist.

Over 300 species of Fucaceæ (including 150 Sargassums) have been distinguished.

Alliance XII.—Dictyotales.

Family: *Dictyotaceæ.*

A small group of Brown Sea-weeds distinguished by the fact that both egg-cells and spermatozoids are destitute of cilia. The sexual cells are contained in club-shaped vesicles, inserted in tufts on the surface of the plants. Asexual reproductive cells ("tetraspores") are formed in sporangia in fours. They include the common *Dictyota dichotoma* and the beautiful iridescent fan-like *Padina pavonia.*

Alliance XIII.—Florideæ, Red Sea-weeds.

Aquatic, for the most part marine, plants, which contain in addition to chlorophyll a red or purple pigment, *phyco-erythrin*; the pigment, as in the brown sea-weeds, is confined to definite corpuscles. Reproduction is by means of asexual spores (tetraspores), and sexually by non-ciliated spermatia and procarps.

With the exception of *Batrachospermum, Lemanea,* and one or two other genera, the Florideæ are marine organisms and inhabit on the whole a deeper zone than any other sea-weeds. Several views prevail as to the significance of the red pigment. As has been already indicated (vol. i. p. 390) the rays of light, useful in ordinary chlorophyll-assimilation, are soon absorbed, as white light traverses considerable strata of water. Such light as penetrates some distance from the surface is preponderatingly blue, and, as is now known, such rays are actually destructive of vegetable protoplasm. It may well be then that the red pigment serves to screen the protoplasm from the action of these rays, permitting the chlorophyll to make use of such of the red rays as filter to it; or—what is more probable—the red pigment is itself an assimilating pigment, either directly absorbing the blue rays and allowing the protoplasm of the chlorophyll-corpuscles to use their energy for building up complex food-materials, or indirectly (as indicated at vol. i. p. 390) by altering their wave-length they are made serviceable to the chlorophyll-corpuscles.

The Florideæ exhibit an enormous variety of form, and almost all of them are attached. There are the delicate cell-filaments of the *Callithamnions,* the corticated *Polysiphonias* and *Ceramiums* so common on our coasts, the fleshy cylindrical *Gracilarias* and *Polyides,* the flat and lobed *Chondrus* and *Gigartina,* the leathery *Iridæa,* and a host of others. One of the most beautiful of British genera is *Delesseria,* with its creeping stalk and crimson leaves with midribs and veins. In some species the leaves are entire, in others their margins are sinuous and lobed. Of all red sea-weeds perhaps the Australian *Claudea* holds the palm for beauty with its large latticed, rose-pink fronds. Certain groups, *Corallina, Melobesia, Lithothamnion,* &c., are encrusted with large amounts of carbonate of lime, and build regular banks and reefs under the sea. In all there are some 280 genera and 1800 species of Florideæ.

Reproduction by means of asexual spores is a common phenomenon in the group. These spores, though not invariably, are most frequently formed in clusters of four,

and are termed *tetraspores*. In the simpler forms they arise in little projecting sporangia, in other cases they are on specialized branches or embedded in the substance of the frond.

The sexual organs, however, are very remarkable, and differ from those of other Thallophytes. The male cells arise from clusters of cells (antheridia) at the tips of branches or in groups upon the surface of the frond. Each antheridium liberates a single, non-ciliated male cell termed a *spermatium*. The female organs or *procarps* consist of a filamentous receptive organ, the trichogyne, and a basal part, the *carpogonium* (*cf.* figs. 204[7] and 204[8], p. 53). Besides the carpogonium there are *auxiliary cells*, to be described directly. The process of fertilization has been followed in detail in *Nemalion* since the earlier portions of this volume passed through the press, and we now know that the suggestion of an osmotic fertilization in the Florideæ (*cf.* p. 60) is erroneous. The spermatium becomes attached to the trichogyne, and at this point the wall of the trichogyne is absorbed. The nucleus of the spermatium enters the trichogyne and travels down it to the carpogonium at the base, where it fuses with the carpogonial nucleus. The carpogonium now divides, giving rise to a mass of spores (the carpospores). In other cases the process is less simple. As before there is a trichogyne and carpogonial cell, but associated with the latter a number of auxiliary cells. The carpogonium when it is fertilized does not give rise at once to a mass of spores, but enters into a process of conjugation with these auxiliary cells, and from them the carpospores arise. This conjugation may be an immediate fusion, or may be brought about by the instrumentality of special tubes. Thus we may suppose the fertilizing influence to be transmitted. In some cases (as in *Dudresnaya*) this may take place over considerable distances, from branch to branch. In the simpler forms the procarps are modified branches projecting freely into the water; in the more fleshy and ribbon-like forms they are sunk in hollows on the thallus and often associated with a large number of auxiliary cells. The trichogyne projects into the water through a small pore in the portion of the surface which roofs over the procarp and auxiliary cells. As a result of fertilization of the carpogonium and its conjugation with the auxiliary cells, a large mass of carpospores arises, which raises up the surface like a blister.

Fossil remains of red sea-weeds occur under the name of Nullipores. These are the calcareous incrustations of the *Corallinas*, *Melobesias*, *Lithothamnions*, &c., mentioned above. They occur in both the secondary and tertiary rocks. The Leitha limestone, largely used for building purposes in Vienna, comes from extensive nullipore banks in the Leitha Mountains, south-west of Vienna on the Hungarian frontier, and, just as in Paris many of the finest buildings are constructed of the consolidated calcareous remains of Foraminiferæ, so in Vienna are the incrustations of certain red sea-weeds put to this purpose.

Class V.—FUNGI.

Parasitic or saprophytic plants destitute of chlorophyll and for the most part possessing a mycelium. Sexual reproduction known and generally admitted in the Phycomycetes only. Asexual reproduction by means of spores and conidia.

Sub-class I.—Phycomycetes.

Mycelium for most part unicellular, tubular, and branched. Sexual reproduction both by conjugation of equivalent cells and by egg-cells.

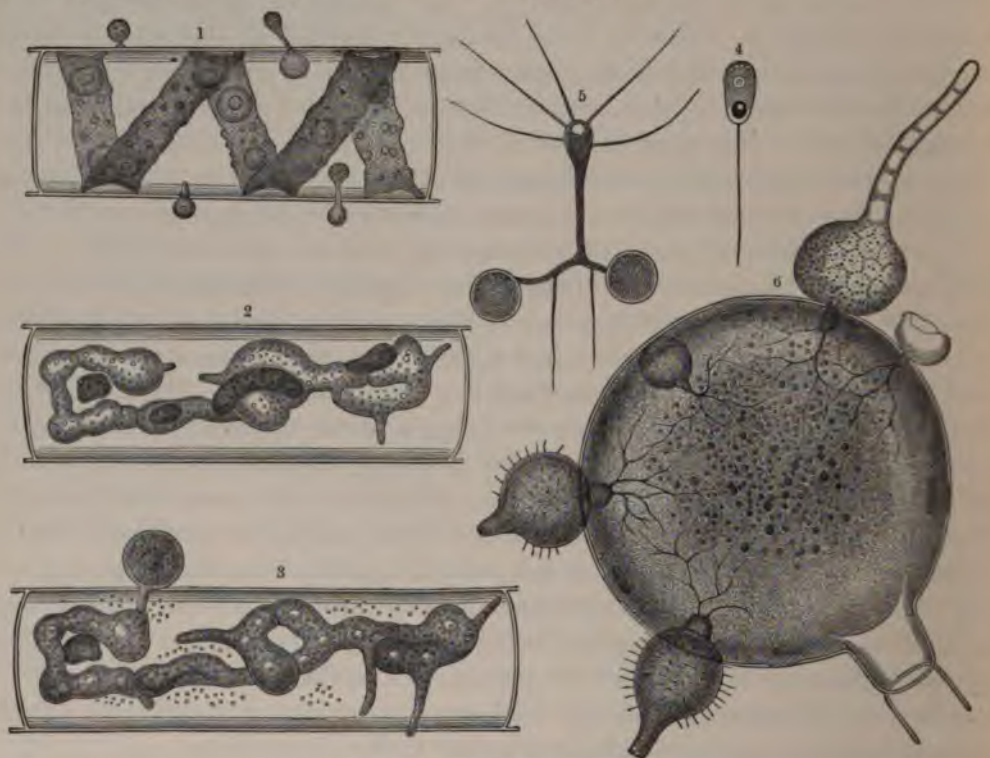


Fig. 379.—Chytridiaceæ and Ancylistaceæ.

1, 2, 3 *Lagenidium Rabenhorstii*, parasitic upon *Spirogyra*. 4, 5 *Polyphagus Euglenæ*. 6 *Rhizidiomyces apophysatus*, parasitic on an oogonium of *Saprolegnia*.

Alliance XIV.—Oomycetes

Families: *Peronosporeæ, Saprolegniaceæ, Chytridiaceæ, Ancylistaceæ, Entomophthoreæ.*

Mycelium often very slightly developed; asexual reproduction by means of swarm-spores; sexual reproduction by egg-cells. On the whole in this group we are dealing with Fungi which very nearly resemble the Algæ of the Alliance Siphoneæ (e.g. *Vaucheria*) both as regards the structure of their mycelium and mode of reproduction. A loss of sexuality is to be noted in many members of this group.

Peronosporeæ.—Are mostly parasitic upon Flowering Plants, and the cause of many destructive diseases. They establish themselves by means of a branching, tubular, non-septate mycelium which penetrates the intercellular system of the host-plant (*cf.* p. 56). They propagate asexually by means of unicellular sporangia borne on branched hyphæ which project from the stomates, &c., of the host (*cf.* fig. 381[2]); these sporangia (or spores as they are sometimes termed) liberate on a moist substratum a number of swarm-spores (figs. 381[4,5,6]) which originate new plants.

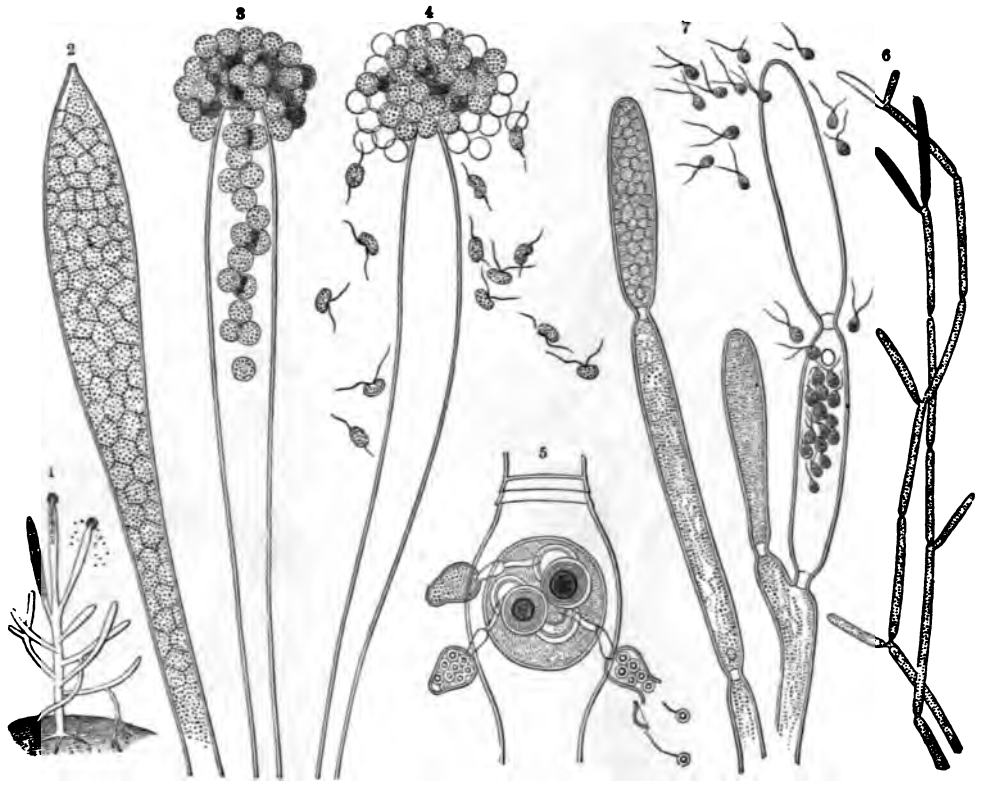


Fig. 380.—Swarm-spores in Saprolegniaceæ and Chytridiaceæ.

[1] *Achlya prolifera.* [2, 3, 4] Successive stages of swarm-spore-formation in *Achlya prolifera.* [5] *Chytridium Olla*, parasitic on the oogonium of the Alga *Œdogonium*; development of swarm-spores. [6] *Saprolegnia lactea.* [7] Development of swarm-spores in the same. (Partly after De Bary and Pringsheim.) [1] ×20; [2, 3, 4] ×400; [5] ×300; [6] ×100; [7] ×300.

Sexual reproduction also takes place by the formation of oogonia and tube-like antheridia. The latter become attached to the former (fig. 381[3]), and, putting out fertilizing tubes which penetrate to the egg-cell within the oogonium, transmit their spermatoplasm. No spermatozoids are differentiated, but the spermatoplasm travels *en masse.* The fertilized egg-cell enters on a resting stage, and when it germinates may either give rise to swarm-spores (e.g. *Cystopus*) or grow at once into a new plant (*Pythium, Peronospora*). To *Phytophthora infestans* is due the well-known Potato-disease. The Fungus attacks the foliage and reproduces abundantly asexually. Later, its mycelium penetrates to the tubers and passes into a dormant state there. Consequently when stored these potatoes go bad, and if

used for planting are liable to reproduce the disease next year. Sexual reproduction is as yet not certainly known to occur in the life-history of the Potato-disease Fungus. *Phytophthora omnivora* and *Pythium de Baryanum* attack and destroy many young seedlings, causing them to "damp off". Various species of *Peronospora* are known which attack large numbers of cultivated plants. *P. parasitica* works havoc amongst the Cruciferæ; *P. viticola* (=*Plasmopara viticola*, fig. 381) has been referred to as a deadly disease on the Vine; *P. Viciæ* on various leguminous

Fig. 381.—The False Vine-mildew, *Peronospora viticola*.

[1] A bunch of grapes attacked by the False Vine-mildew. [2] Spores or conidia on branched hyphæ projecting from a stoma of a Vine-leaf. [3] Fertilization. [4] A single conidium. [5] Swarm-spores arising within the conidium. [6] A single swarm-spore. [1] nat. size; [2]×80; [3–5]×350; [6]×380. ([3–6] after De Bary.)

crops; *P. Hyoscyami* on Tobacco-plants, besides which there are many others. The effects of *Cystopus candidus* have already been mentioned (p. 525); it is common upon cruciferous plants.

About 100 species of Peronosporeæ have been distinguished.

Saprolegniaceæ.—Are all aquatic and for the most part saprophytic; a few are parasitic on fish. In structure they much resemble Peronosporeæ. Swarm-spores are liberated in large numbers from the enlarged ends of the hyphæ (fig. 380). Sexual organs arise much as in Peronosporeæ, but although the antheridia develop fertilizing tubes in several instances, no case has been observed in which an actual transfer of spermatoplasm occurs. As a rule several or many egg-cells are produced

in the oogonia (fig. 382), and these germinate parthenogenetically. Although the sexual organs are still preserved in this group their function has been lost, leading the way to their complete atrophy in many other groups of Fungi. Many members of the group occur upon the bodies of dead insects and fish (*e.g.* various species of *Saprolegnia, Achlya, Aphanomyces*). *Aphanomyces phycophilus* is parasitic upon Algæ (e.g. *Spirogyra*) and *Saprolegnia Ferax* upon Salmon, &c.

About 45 species have been distinguished.

Chytridiaceæ.—Small parasitic aquatic Fungi whose mycelium is almost entirely wanting; they produce characteristic sporangia which liberate uniciliate swarm-spores. *Polyphagus Euglenæ* develops a very delicate mycelium, of which the branches become attached to Euglena-cells (fig. 379 [5], two Euglenas are thus attacked), and from the central portion of the mycelium arises a sporangium from which uniciliate swarm-spores (fig. 379 [4]) are liberated. These in turn germinate, develop threads, and entangle fresh Euglenas. *Rhizidiomyces* attacks the oogonia of Saprolegnias, sending a branching mycelium into their interior (fig. 379 [6]) and producing a pear-shaped sporangium at the surface which liberates numerous swarm-spores. *Chytridium Olla* (fig. 380 [5]) produces its sporangia on the oogonia of *Œdogonium*; its swarm-spores escape by the removal of a lid.

Over 180 species are known.

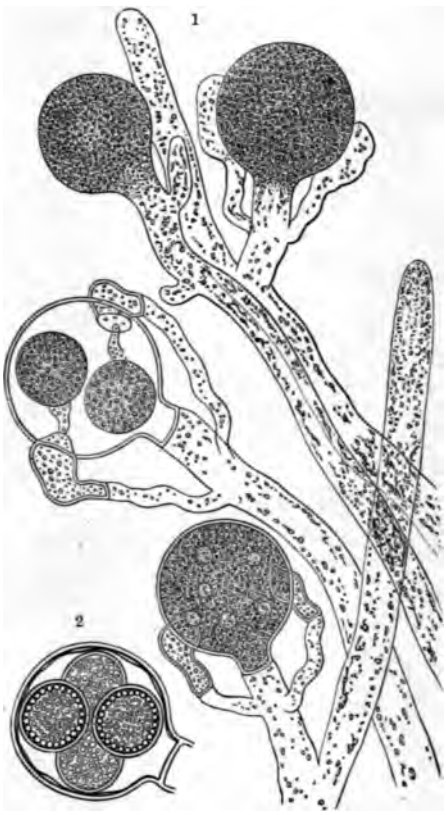


Fig. 382.—*Achlya lignicola.*

[1] Oogonia with antheridia and fertilizing tubes; no fertilization happens, however. [2] An oogonium containing egg-cells which have put on cell-walls without being fertilized. [1] and [2] × 400. (After Sachs.)

Ancylistaceæ.—Very nearly resemble the Chytridiaceæ in mode of life, but differ in exhibiting sexuality. *Lagenidium Rabenhorstii* attacks cells of *Spirogyra*, &c. The spores become attached to the *Spirogyra*-cells, and penetrate the wall (fig. 379 [1]) by means of a tube which branches about within, forming a lobed, irregular body (fig. 379 [2]), which may open at the outside, liberating swarm-spores (fig. 379 [3]), or sexual organs may arise inside and fertilization take place.

14 species have been distinguished.

Entomophthoreæ.—A group of forms almost all of them parasitic on insects. They are adapted to non-aquatic life, and connect the Peronosporeæ with the Zygomycetes.

The tubes of these parasites having effected an entrance into the body of an

insect, bud and sprout there with great activity. *Entomophthora radicans* commonly attacks caterpillars of the Cabbage-white (*Pieris Brassicæ*). Having spread through its interior, it sends out tufts of hyphæ on the ventral side (fig. 383[1]), thus rooting the caterpillar to the substratum. It now develops hyphæ all over the body wrapping up the caterpillar like a mummy (fig. 383[2]). At the tips of these hyphæ conidia are abstricted and shot off to some little distance (figs. 383[3, 4, 5]). A con-

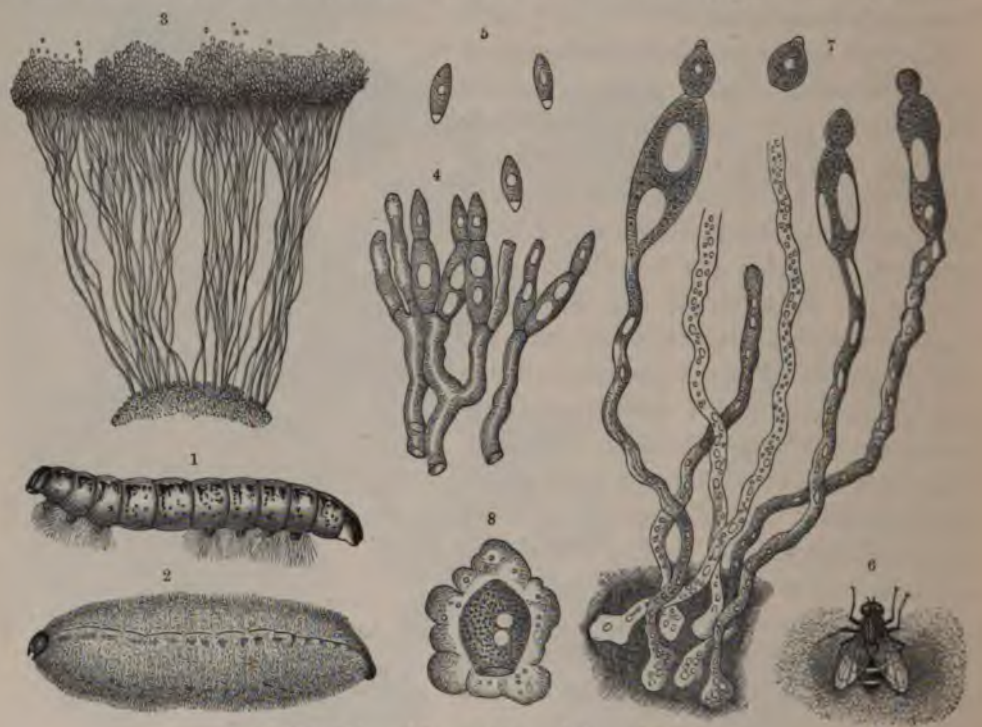


Fig. 383.—Entomophthoreæ: *Entomophthora* and *Empusa*.

[1] A caterpillar of the Cabbage-white Butterfly attacked by *Entomophthora radicans*. [2] The same caterpillar fully invested by the Fungus. [3] Tufts of conidia-bearing hyphæ from the back of the caterpillar. [4] Conidia separating from the tips of the hyphæ. [5] Disarticulated conidia. [6] A Fly attacked by *Empusa Muscæ*. [7] Hyphæ of *Empusa Muscæ*, from the tips of which conidia are being shot off. [8] Conidium inclosed in sticky mucilage. [1, 2, 6] nat. size; [3] ×80; [4, 5, 7] ×300; [8] ×630. (After Brefeld.)

jugation of branches sometimes occurs, whilst in other cases fruits are formed parthenogenetically. *Empusa Muscæ* produces a disease common amongst flies in the autumn. The Fungus having effected an entrance into the body of a fly gradually fills it up with its sprouts. In due time tubes penetrate the surface and develop conidia at their extremities (fig. 383[7]). These are shot off as in the last case, and one may often see flies stuck to the window-pane in autumn surrounded by a halo of these conidia (fig. 383[6]).

About 80 species of Entomophthoreæ are known.

Alliance XV.—Zygomycetes.

Families: *Mucoraceæ, Mortierelleæ.*

Are mould-like saprophytes with a much-branched, non-septate mycelium, sexual reproduction by conjugation; swarm-spores never met with. The common *Mucor Mucedo* (fig. 384) may be regarded as typical of this group. Its mycelium establishes itself on the substratum, and develops long-stalked sporangia at various points on its surface (fig. 384[1]). In each sporangium (fig. 384[2]) numerous spores are contained, and these can germinate, producing new mycelia on a suitable substratum. A conjugation of branches of the mycelium leading to the production of a fruit or zygospore (fig. 384[3]) occasionally takes place, but the sexual method of reproduction is much commoner in other members of the group (*cf.* pp. 53, 54). The zygospore (or zygote) is invested in a strongly thickened membrane and can remain dormant for a considerable period. The hyphæ in many of the Mucors can break up into continuous chains of cells which disarticulate and propagate the plant; these offshoots are known as chlamydospores or gemmæ.

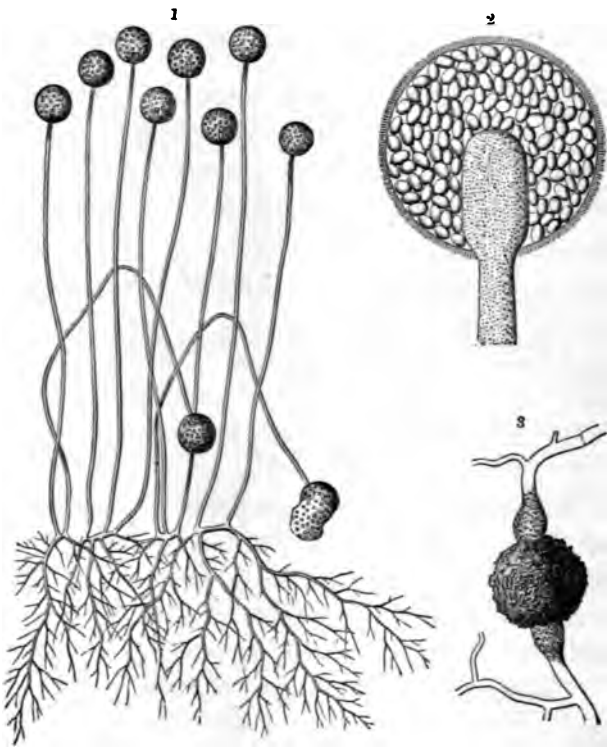


Fig. 384.—*Mucor.*

[1] Mycelium with stalked sporangia; ×40. [2] A single sporangium; ×200. [3] A zygospore produced by conjugation; ×160.

It often happens amongst the Mucors that although the conjugating branches are produced, they do not conjugate but each produces a fruit parthenogenetically. These, in contradistinction to zygospores, are called "azygospores". Or, as in *Mucor tenuis*, the "conjugating branches" no longer arise in pairs but isolated; these also form azygospores. Thus in this group, as in the Saprolegniaceæ of the alliance Oomycetes, we note a tendency for sexuality to become obsolete (*cf.* p. 670). A good deal of variety exists in the Mucoraceæ in the arrangement of the sporangia. In *Thamnidium* the sporangial branch ends in a large sporangium, and in addition bears laterally a number of tiny sporangia (sporangioles) containing four spores each, whilst in *Chætocladium* there is a further reduction, and the sporangioles contain

but a single spore. Whilst the bulk of Mucoraceæ are saprophytes on animal excreta, &c., a certain number are parasitic on Mucor itself as well as other Fungi.

The *Mortierelleæ*, though in general resembling Mucoraceæ, are distinguished by the fact that their zygospores become invested in a plexus of mycelial hyphæ which form a sort of pericarp around the fruit. The base of the sporangial hypha also is invested in a sort of bird's-nest. This condition is of interest as it leads on to the more complex fruits of higher Fungi.

The Zygomycetes include 125 species.

Sub-Class II.—Mesomycetes.

Mycelium multicellular; asexual reproduction alone is known by means of spores (not limited in number) developed in sporangia; or by conidia. They are regarded as occupying an intermediate position between the lower Fungi and the two large groups of higher Fungi, the Ascomycetes and Basidiomycetes respectively.

Alliance XVI.—Hemiasci.

Tube-like sporangia containing an unlimited number of spores. This alliance leads on to the Ascomycetes.

Families: *Ascoideæ, Protomycetes, Thelebolæ.*

These are mostly simple forms of parasites characterized by the indefinite number of spores contained in their sporangia. Some of them produce chlamydospores freely. *Thelebolus* is interesting in that its sporangium is inclosed in a cortex and may be compared with *Mortierella* of the Zygomycetes on the one hand, and with the corticated Ascomycetes (carpo-asci) on the other.

There are about 20 species belonging to this alliance.

Alliance XVII.—Hemibasidii.

Parasites with a septate mycelium, which forms numerous chlamydospores. From these spores a promycelium is developed on which conidia (sporidia) are produced. No sporangia are formed. This alliance is thought to lead on to the Basidiomycetes.

Families: *Ustilaginaceæ, Tilletiaceæ.*

These are all parasitic forms, and are known as the Smuts. The mycelium grows in the living tissues of the host, and concludes its development with the production of chains of chlamydospores (cf. p. 673), which are provided with a thick membrane, and are usually dark in colour. It is in respect of this character that the name "Smut" has been given. Very often these chlamydospores are produced in connection with the fruiting organs of the host-plant (various Grasses, &c.). The

chlamydospores only germinate after they have been distributed, and in a very characteristic manner. A short tube is formed, and from this (the promycelium or *basidium*, *cf.* p. 674) conidia (=sporidia) are abstricted. In the Ustilaginaceæ this basidium is septate and the conidia are abstricted *laterally*; in the Tilletiaceæ the basidium is non-septate, and the conidia are abstricted as a crown at the apex. This is the main difference between the two families. The conidia, which are budded off from the promycelium, have the power of budding in a suitable soil with enormous facility, forming new conidia, and this may be continued for a considerable time. In this way the soil becomes thoroughly infected, and should a young seedling host-plant arise, it is almost certain to be penetrated and invaded by one of these germ-like conidia.

Ustilaginaceæ.—These are the Smut-fungi properly speaking. *Ustilago segetum* (= *Ustilago carbo*), the common Smut of Wheat, Barley, Oats, &c., has been very fully investigated. The cereals in question become infected when quite young by the tiny conidia, which put out delicate germinal tubes and penetrate the young growing tissues. Should the young plants escape infection at this stage, they are safe against the parasite, which cannot penetrate the hard, adult tissues. The tubules of the *Ustilago* penetrate from cell to cell, and take up their position at the growing point. Here they keep pace with the growth of the host, but the presence of the parasite is not manifest externally until the grain begins to ripen. As the grains begin to swell, the fungus increases rapidly, and occupies the greater portion of their substance with its mycelium. It thrives, of course, at the expense of the food which would otherwise have served in forming the embryo and reserve of food-material in the seed. Finally, the Fungus resolves itself into masses of black chlamydospores—the "smut"—which appear between the glumes of the ear. These chlamydospores, as already stated, after a period of rest, produce their promycelia and bud off conidia, which in turn bud off other conidia, and so the ground is kept infected. It was formerly a matter of mystery how the Fungus got into the host-plant, as traces of it were not recognized till it burst out in the ripening ear in the "smut" stage. It is only comparatively recently that the period of infection has been recognized, and the fact that the mycelium grew up, so to speak, with the host-plants was fully realized. *Ustilago Maydis* produces hypertrophied growths on the Maize, and has been alluded to in a former chapter (cf. p. 524). *Ustilago violacea* attacks the stamens of many Caryophyllaceæ, developing its chlamydospores in place of pollen in the anthers. *Ustilago longissima* is very common in the leaves of the aquatic Grasses *Glyceria aquatica* and *G. fluitans*; it produces its chlamydospores as long, parallel, black lines.

More than 60 Ustilagos have been distinguished; a large number of them attack cereals and other grasses.

Tilletiaceæ.—Have on the whole a life-history resembling the Ustilagineæ; their main point of difference residing in the fact that the promycelium is unsegmented, and produces its conidia in a crown at the apex. *Tilletia Tritici* attacks wheat. In *Urocystis* the spores are clustered into little balls, the accessory spores forming a

sort of cortex around the central spore which germinates as in *Tilletia*. *Urocystis Violæ* is common on the leaf-stalks and blades of Violets.

About 100 species of Tilletiaceæ have been distinguished.

Sub-class III.—Mycomycetes.

Mycelium many-celled. Reproduction asexual, either by spores of limited number in asci, or by conidia of limited number on basidia.

Alliance XVIII.—Ascomycetes.

Parasitic (or saprophytic) Fungi, producing spores in special tubular sporangia, the *asci*. These spores, termed *ascospores*, do not exceed 8 in number. In addition to the asci there are subordinate conidial fructifications.

Families: *Exoascaceæ*, *Perisporiaceæ*, *Pyrenomycetes*, *Discomycetes*.

As stated, this alliance is characterized by the possession of sporangial fructifications, consisting of tubular asci containing as a rule 8 ascospores. A number of such asci are shown in fig. 388[2] with sterile supporting hyphæ, the paraphyses, between them. In addition to these ordinary and typical ascus-bearing fructifications, secondary fructifications producing conidia or chlamydospores are largely met with; consequently many of these Fungi appear under several forms in addition to the ascus stage. The Ascomycetes are divided into families according to the characters of the ascus-fruit. In the *Exoascaceæ* the asci are borne freely and exposed on the mycelium; in the other three families in special receptacles. In the *Perisporiaceæ* the group of asci is contained in a nut-like or tuber-like body; in the *Pyrenomycetes* the asci are produced in special pear-shaped excavations in a solid tissue which open by a pore to the exterior; in the *Discomycetes* the receptacle forms an open plate or cup, or sometimes an irregular body covered with the layer of asci.

Exoascaceæ.—This family comprises the parasitic genera *Exoascus* and *Taphrina*, the gall-like deformations caused by which were so fully described on pp. 524 and 527. The tissues of the host-plants are penetrated by the mycelia of these forms, and the asci are produced over the surface of the parts attacked, generally bursting through the cuticle of the epidermis. Each ascus contains 8 spores, but in many species many more than this number are often found; this is due to the fact that the 8 original ascospores begin to bud whilst still within the ascus, producing a large number of secondary spores (conidia). *Exoascus* has a perennial mycelium, and to its species are due a large number of the "witches'-brooms" and other hypertrophies. *E. Pruni* produces the "pocket-plum" (*cf.* p. 524); *E. Alni-incanæ* the curiously altered Alder catkins represented in fig. 358[1] (p. 523); *E. Carpini* the birds'-nest-like witches'-brooms of the Hornbeam; *E. deformans* the "curl" of Peach-leaves. *Taphrina* is largely a leaf-parasite, and its mycelium is not perennial. *T. carnea* causes blisters on the leaves of the Birch.

About 50 species of Exoascaceæ have been distinguished.

Perisporiaceæ.—Here are included all forms in which the asci are inclosed in fruit-like bodies, *i.e.* the Mildews, Moulds, and Truffles.

The Mildews are chiefly leaf-parasites, and spread their mycelium over the surface of the foliage and send their suckers (or haustoria) into the epidermal cells (*cf.* fig. 32[2], vol. i. p. 165). In due time they produce their ripe ascus-fruits like tiny black grains scattered over the surface of the leaf. Each of these fruits consists of a shell-like investment inclosing one or more asci, each of which contains 8 spores. *Sphærotheca* is the simplest form, there being but a single ascus in its fruit. *S. pannosa* is the Rose-mildew, and *S. Castagnei* the Hop-mildew, a very destructive parasite in Hop-growing districts. *Erysiphe* has several asci in its fruits, and includes the well-known *E. Tuckeri*, the true Mildew of the Vine (to be distinguished from *Peronospora viticola*, figured on p. 670, which is the false Mildew). A tropical genus of leaf-parasites allied to our Mildews is *Meliola*, which is widely distributed.

The Moulds include several exceedingly common saprophytes which make their appearance on the most various sorts of organic matter. The Blue Moulds, which occur on jam, bread, leather, &c., are probably the best known and most commonly recognized of all the smaller Fungi. These forms spread their mycelia over any suitable substratum, and penetrate it with their hyphæ. Their usual fructification is not the ascus-fruit, but clusters of conidia, borne on erect hyphæ, which stand out from the mycelium. Two common Moulds are represented in fig. 193, p. 18. *Aspergillus niger* (figs. 193[4] and 193[5]) bears its conidia in spherical tufts on enlarged aërial hyphæ. The swollen end of an aërial hypha is densely set with cylindrical cells, from which the conidia are abstricted one after another. *Penicillium crustaceum* (figs. 193[8] and 193[9]) is very similar, but here the conidia are borne on a hypha which branches near its extremity like a compound umbel. Another form, *Eurotium*, is shown in fig. 385[7], p. 679. The ascus-fruits of these Moulds are not very conspicuous, nor are they always very plentifully developed. They arise on the mycelium after the conidial stage is over, and when ripe are about the size of small shot. They commence by the entwining of certain hyphal branches (*Penicillium*, fig. 193[6], p. 18; *Eurotium*, fig. 385[9], p. 679) which have been regarded as representing male and female organs (*cf.* p. 60). That fertilization takes place is strenuously denied by many modern mycologists, and the sexual nature of the entwining hyphæ is not universally recognized. Be this as it may, the result of the process in question (which also takes place in the Mildews) is the formation of a sinuous hypha, which becomes embedded in a dense cortical sheath which grows up from the mycelium close by the place of origin of the entwined hyphæ. This is the young fruit-body; that of *Eurotium* is shown in section in fig. 385[10]. From the central hypha numerous asci, each containing 8 spores, are ultimately developed (figs. 193[7] and 385[11]). The ripe ascus-fruit, which frequently takes several months to mature, consists of a hard outer shell containing numerous asci (one of these fruits is shown in fig. 385[7], in the right-hand bottom corner); it is

able to remain dormant over long periods. *Aspergillus* is sometimes parasitic, and is stated to promote a diseased condition of animal tissues known as *mycosis*. *A. fumigatus* is found growing spontaneously in the air-passages of birds and in the human lungs.

Tuberaceæ.—These are subterranean saprophytes whose mycelia grow in humus. Their fructifications are solid, tuber-like bodies of various sizes. The Truffles (*Tuber rufum, T. melanosporum, T. æstivum,* &c.) are well-known, and several of the species are esteemed as delicacies. In section the Truffle-fruit shows a curious mottled appearance due to its irregular chambered character. The chambers are filled with hyphæ which produce numerous oval asci, each containing 4 spores (*cf.* fig. 387 [1], which represents an enlarged chamber); the spores are covered with delicate spines. The wall of the fructification consists of a hard parenchyma-like layer, and possesses a rough and warted exterior. As the fructification ripens the mycelium disappears, the Truffles being found detached in the soil. The spores are ultimately liberated by the decay of the fruit. *Elaphomyces* produces fruits about the size of a nut. The mycelium of species of this genus is concerned in the formation of the fungal investment or mantle of the roots of Pine-trees known as mycorhiza (*cf.* vol. i. pp. 249, 250); in the Amentaceæ, &c., neither the species nor group to which the Fungi forming this mantle belong has been ascertained.

Pyrenomycetes.—An extremely large and varied group, including both parasitic and saprophytic forms. The essential character of the family is the presence of flask-shaped chambers with a pore at the apex in which the asci are produced. The chambers, the *perithecia,* may be either solitary upon the mycelium in the simpler forms or embedded in receptacles of most varied form (the stromata) in the more complex. Sections of perithecia are shown in figs. 385 [5] and 386 [5]. A great many Pyrenomycetes possess conidial as well as ascus-fructifications. The conidia may arise in tufts from the surface of the mycelium or in urn-shaped cavities—not unlike perithecia—which have been termed *pycnidia.* As a rule, the conidial precedes the ascal stage. This variety in fruiting has led to the recognition of several forms, which are only stages in the life-history of one Fungus. Consequently, as knowledge extends, many of these supposed species have to be suppressed.

Among the simpler forms may be mentioned *Podospora,* which produces solitary sessile perithecia upon its mycelium. *Polystigma rubrum,* which occurs on the leaves of species of Cherry and Plum, produces a brilliant red spotting on the leaves. The mycelium permeates the internal tissues, and during the summer the conidial receptacles or pycnidia are formed. Later, usually in the following spring, in the fallen leaves, the perithecia arise, and the ascospores now liberated infect the young foliage in the vicinity. *Nectria cinnabarina,* another fairly simple form, occurs as little red cushions on the branches of Horse-Chestnut, Elm, Sycamore, &c.; these cushions burst through the bark budding off conidia (this is the bright red stage), whilst later, as tiny lobes, the perithecia arise upon them, each lobe containing a single perithecium (this is the dull crimson stage). The number of simple parasitic Pyrenomycetes is almost endless.

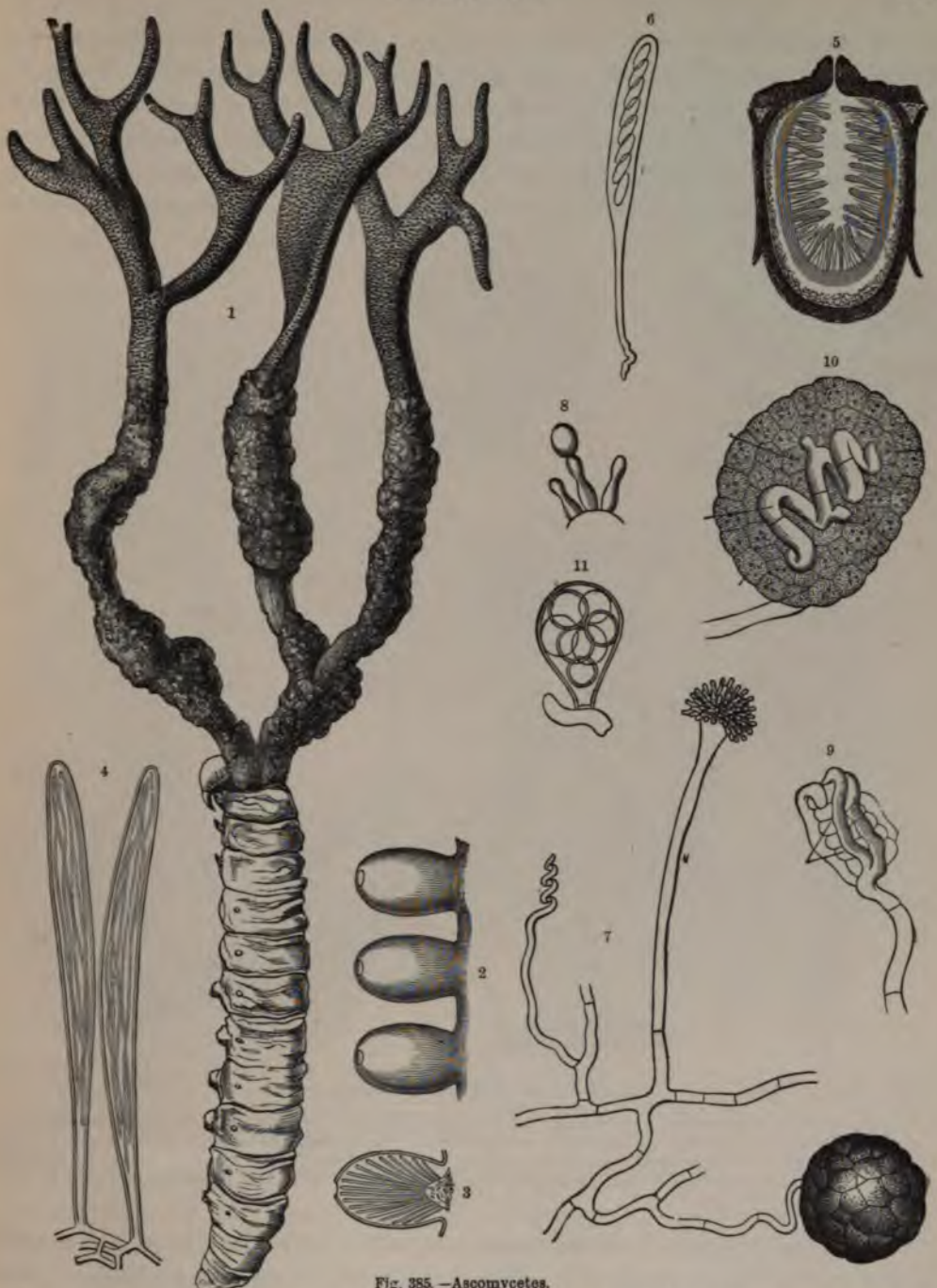


Fig. 385.—Ascomycetes.

1 *Cordyceps Taylori*, a pyrenomycetous Fungus which attacks caterpillars; the branched antler-like stroma has developed from the sclerotium, and its lower warted portion bears the perithecia. 2 Three perithecia; enlarged. 3 A perithecium in section. 4 Two asci containing filamentous spores. 5 Vertical section of a perithecium of *Xylaria Hypoxylon*. 6 Ascus of same. 7 Mycelium of *Eurotium* bearing a conidial hypha (to right, above), a commencing fruit (to left), and a ripe ascus-fruit (to right, below). 8 A conidium of the same being abstricted. 9 Entangled hyphæ from which a fruit arises; the spiral central hypha has been interpreted as a female organ, the tubes growing up the side as male. 10 A young fruit of the same in section; the asci arise later from the large coiled central hypha. 11 A single ascus of *Eurotium*. 1 nat. size; 2, 3, 5 × 50-90. 4, 6 × 500; 7 × 190: 8-11 × 250.

Of complex forms with stromata we may mention *Cordyceps*, *Xylaria*, and *Claviceps*. *Cordyceps militaris* and other species attack caterpillars. The germ-tube having once effected an entrance into the body of the caterpillar and established itself in the superficial layers begins to sprout vigorously, these sprouts being carried in the blood to all parts of the body. The sprouts now grow into hyphæ, and gradually the whole caterpillar is replaced by a dense fungal tissue which

Fig. 386.—The Ergot of Rye, *Claviceps purpurea*.

[1] Ear of Rye showing two sclerotia of the Fungus. [2] Conidia arising from the mycelium which develops around the ovary. [3] Stalked stromata arising from the sclerotium. [4] Longitudinal section through the head of a stroma showing the perithecia at the edge. [5] Vertical section through two perithecia showing the asci. [6] Asci. [7] Ascus liberating its filamentous spores. [8] Filamentous spores. [1], [3] nat. size; [2] ×200; [4] ×40; [5] ×50; [6] and [7] ×700; [8] ×750. (Partly after Tulasne.)

maintains outwardly the form and appearance of the caterpillar, although of animal substance but little traces are left. This fungal mass is known as a *sclerotium*, and it can remain dormant for some time. Ultimately a branching stroma arises from the sclerotium (*Cordyceps Taylori*, fig. 385 [1], p. 679), or, in *C. militaris*, several club-shaped stromata. These remarkable stromata are covered with little papillæ on their lower portion, and each of these papillæ corresponds to a perithecium (figs. 385 [2] and 385 [3]). The spores in the asci are long and slender (*cf.* fig. 385 [4]). A

Pyrenomycete which produces an antler-like stroma resembling that of *Cordyceps Taylori*, and which is exceedingly common on old tree stumps, is *Xylaria Hypoxylon*. Indeed, the stroma represented in fig. 385 [1] would almost do for that of this *Xylaria*. It is purplish in colour below where the perithecia are borne; at the tips it passes over into a glaucous grey colour, this bloom being due to the conidia, which are abstricted in this region. Another curious fingered species, *X. polymorpha*, is also met with in similar situations. *Claviceps purpurea*, the Ergot

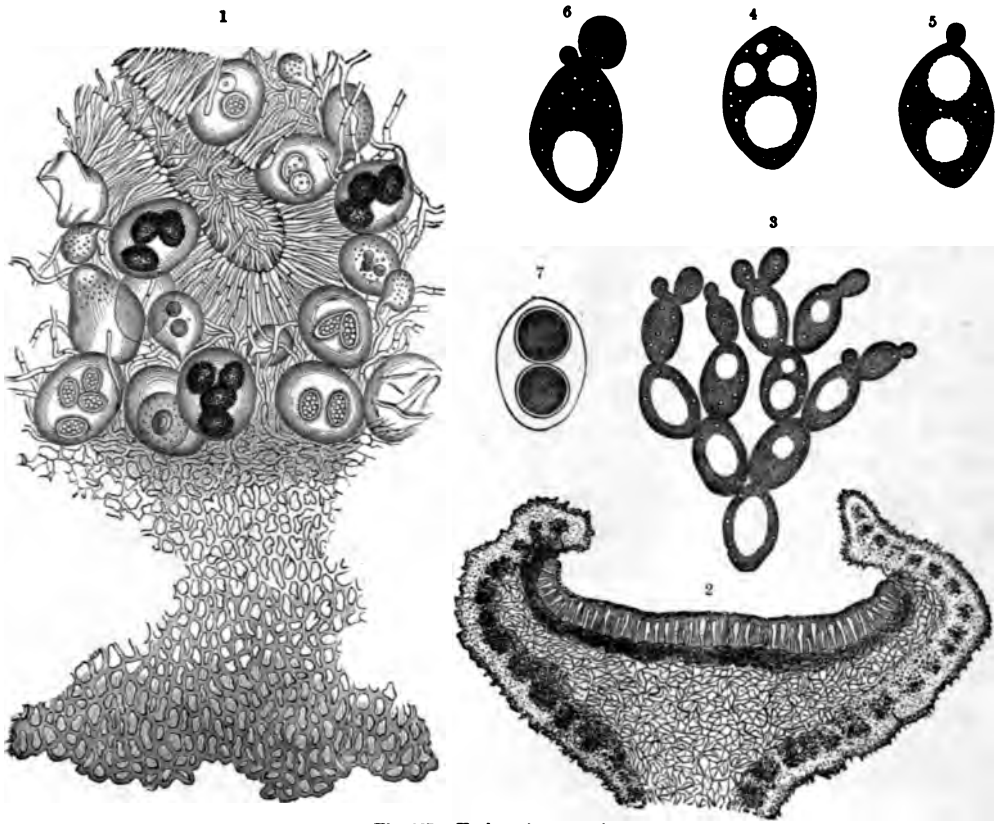


Fig. 387.—Various Ascomycetes.

1 Section through part of a Truffle (*Tuber melanosporum*) showing a portion of the cortex (below) and a chamber containing oval asci, each of which contains 4 spores. 2 Vertical section of the apothecium of a discomycetous Lichen, *Physcia ciliaris* (after Sachs). 3 The Yeast-plant, *Saccharomyces cerevisiæ*. 4, 5, 6 Single Yeast-cells showing development of a sprout. 7 A cell containing two spores. 1×200; 2×60; 3×600; 4–7×1000. (Partly after Rees.)

of Rye and other grasses, is a very interesting form. The spores attack the ovaries of Grasses and invest them with a mycelium from which conidia are abstricted in large numbers (fig. 386 [2]). These can at once infect new plants. Gradually the whole ovary is replaced by a mass of fungal substance, the sclerotium. In the autumn at the time of harvest the ears of Rye may be seen with these dark sclerotia projecting from them (fig. 386 [1]). Care has to be exercised that they do not get mixed up with the grain, as the Ergot contains an alkaloid and other poisonous substances, and if intermingled with food causes a disease which has received the name of ergotism. The sclerotia remain dormant through the winter,

but in the spring give rise to their stromata, which consist of a number of orange-coloured spherical bodies borne on purple stalks. A germinated sclerotium is shown in fig. 386 [3]. The head bears the perithecia at its periphery (figs. 386 [4] and 386 [5]), and in these are contained the asci with their filamentous spores (figs. 386 [6, 7, 8]).

In addition to the forms enumerated above, a large number of pyrenomycetous Fungi are found always associated with Algæ into symbiotic communities known as *Lichens* (*cf.* vol. i. p. 244). Though in a strict systematic review these forms should be noted here, still, as Fungi from at least two other groups occur in similar relations to Algæ, it will be convenient to treat them all under one heading, rather than scattered over the alliances with which they have a natural affinity (see *Lichenes*, p. 691).

Discomycetes.—These, like the Pyrenomycetes, constitute a very extensive family. They are characterized by the fact that when mature the structure bearing the asci expands into a disc or cup, so that the ascal surface is exposed; or this surface is spread over the outside of a fleshy receptacle.

As a good example of a Discomycete, the large genus *Peziza* may be cited. They are met with chiefly on decaying vegetable matter, and in the various species the disc or cup—the fertile receptacle—is sessile on the mycelium. *Peziza vesiculosa* (*cf.* fig. 388 [5]) is one of the commonest British species, occurring in humus, rotting leaves, &c. Its cups (the apothecia) attain a diameter of 2–3 inches, are buff in colour, fleshy, and very fragile. The inside of the receptacle is everywhere lined with the layer of asci, with sterile hairs, the paraphyses, between (it is similar to fig. 388 [2]). Another common species is *P. scutellata*; it forms little flat red discs about the size of sixpenny-pieces upon rotting wood, and the margin is set with hairs. Several of the Pezizas are stalked (*cf.* figs. 388 [3] and 388 [4]). *P. æruginosa* is an interesting form; it also is stalked, and grows especially upon dead branches of Oak. It permeates the wood with its mycelium, and this appears to excrete a green pigment which stains the wood in its vicinity. The stalked apothecium is also green in colour. This green-rotting wood is exceedingly common and is used in the manufacture of "Tunbridge ware"; the actual Fungus, however, is by no means so obvious, and from the majority of green-rotted branches not only has the apothecium disappeared, but the mycelium also. Resembling a *Peziza*, but very gelatinous, is *Bulgaria inquinans*, common on decaying trunks of trees. *Peziza Willkommii*, causing the Larch-canker, has been already referred to (*cf.* p. 522). Nearly related to the Pezizas, and causing parasitic diseases of plants, is *Sclerotinia*. It possesses a well-marked sclerotium, from which stalked Peziza-like apothecia are produced. A species not uncommon in this country is *Sclerotinia tuberosa*. It attacks the underground parts of Wood Anemones and forms its sclerotia in the tubers of this plant. In the spring, instead of Anemone-flowers coming up, the sclerotium gives rise to a number of long-stalked apothecia which appear just above the surface of the ground.

Other more complex Discomycetes are the Helvellas and Morels, forms purely saprophytic. *Helvella* produces a stalked receptacle, curiously folded (see figs. 388 [6]

and 388[7]) and plaited; the whole of the exposed surface of this receptacle is covered with asci. The Morel (*Morchella esculenta*, fig. 388[1]) possesses a thick stalk bearing a large fleshy receptacle marked out in pitted areas. Nearly allied is the genus *Geoglossum*, possessing club-shaped receptacles, black in colour, and covered with asci. *G. difforme*, 2–4 inches high, is often met with among grass in the autumn.

The *Lichenes* belonging to this family are treated with the other Lichens at p. 691.

Reference to a small group of forms, the *Saccharomycetes* or Yeasts, may be

Fig. 388.—Discomycetes.

[1] The Morel (*Morchella esculenta*). [2] Vertical section of the fertile surface of the Morel showing five asci with their spores and filamentous paraphyses between the asci. [3] *Peziza* (*Helotium*) *Tuba*. [4] *Anthopeziza Winteri*. [5] *Peziza vesiculosa*. [6] *Helvella infula*. [7] *Helvella fistulosa*. [1, 4, 5, 6, 7] nat. size; [2] ×4; [3] ×120.

introduced here. They constitute a detached family with ascomycetous affinities, and characterized by their very peculiar mode of life. For the most part they do not form mycelia, but increase by budding and by the formation of spores. *Saccharomyces cerevisiæ* is the well-known Brewer's Yeast. The cells are oval and colourless, and provided with one or more conspicuous vacuoles; the cell-nucleus is not readily demonstrable, though there is little doubt of its existence. Growth here is by budding, little processes being pushed out at the periphery at one or more spots and gradually enlarging (figs. 387[4, 5, 6]); ultimately they are cut off from the parent-cell by the completion of the membrane across the point of union. In this

way groups of cells may hang together in chains (fig. 387[3]) for a short time, but they disarticulate sooner or later. As the substratum becomes exhausted the cells exhibit a tendency to form spores in their interior (2–8), the cell being as it were transformed into an ascus (fig. 387[7]). The special physiological activity associated with this and several other species is alcoholic fermentation (*cf.* vol. i. p. 506), *i.e.* the splitting up of sugar into alcohol and carbonic acid. *S. cerevisiæ* is used in brewing, *S. ellipsoideus* causes the fermentation in the juice of the Grape. *S. mycoderma* forms a scum on wine and beer, and is of interest in that it produces mycelial tubes.

In all there are some 40 species of *Saccharomyces*.

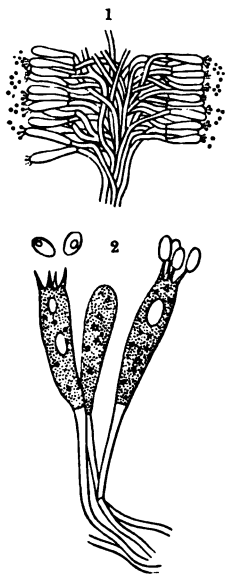


Fig. 389.

[1] Portion of a lamella of an *Agaricus* with a basidial layer (from which conidia are being budded off) on either side. [2] Shows three basidia, more highly magnified, from the basidial layer of the same fungus; conidia are being abstricted from the four processes (sterigmata). [1] ×200; [2] ×500.

Alliance XIX.—Basidiomycetes.

Parasites and saprophytes, reproducing by means of conidia which arise on basidia in definite number. Besides these characteristic conidia there are subordinate fructifications.

Families: *Uredineæ, Auriculariaceæ, Tremellaceæ, Pilacraceæ, Dacromycetes, Hymenomycetes, Gasteromycetes.*

The Basidiomycetes are an exceedingly large alliance, and include forms from the simplest to the most complex. They all agree, however, in the production of conidia from a definite *basidium*, a character which gives its name to the group. As has been already pointed out (p. 674) there are two families in the Hemibasidii, *i.e.* the Ustilaginaceæ and the Tilletiaceæ. In both families a promycelium or basidium arises from the chlamydospore; in the former it is septate and conidia are cut off laterally, in the latter it is non-septate and the conidia are produced in a tuft at the extremity. In the Uredineæ a basidium arises from each cell of the teleutospore (the probable equivalent of a chlamydospore), and this basidium is transversely septate, four cells being cut off at the end of the tube away from the spore. Each of these cells produces a little process, and from each process a conidium is abstricted. In all the other families of Basidiomycetes the teleutospore (or chlamydospore) is suppressed, and the basidia are directly continuous with the hyphæ of the Fungus. Otherwise, the basidia of Auriculariaceæ, Tremellaceæ, and Pilacraceæ, all belong to the type of the Uredineæ, and are derivable from the *Ustilago*-form. On the other hand, the basidia of Hymenomycetes and Gasteromycetes, and probably also of Dacromycetes, belong to the *Tilletia* type (*cf.* p. 675). The conidia do not arise laterally, but from four processes at the tip of an unsegmented basidium (see figs. 389[2] and 390[7]). The very general restriction of the number of processes arising on the basidium to four is without doubt a feature of some importance, and

is a further justification for the inclusion of all these families—at first sight so different—in a single alliance.

Uredineæ.—These are the Rust-fungi, parasites for the most part on the foliage of higher plants. They are outwardly manifest in the form of yellow or brown

Fig. 390.—Basidiomycetes.

[1] *Clavaria aurea.* [2] *Dædalia quercina.* [3] *Marasmius tenerrimus.* [4] *Marasmius perforans.* [5] *Craterellus clavatus.* [6] *Amanita phalloides.* [7] A portion of the basidial layer of the last-named Fungus showing the sterigmata and conidia. [8] *Hydnum imbricatum.* [9] *Polyporus perennis.* [7] ×250; the rest nat. size.

spots and streaks, due to the spores, which are formed in masses on the surface. The mycelium inhabits the intercellular system of the host-plant, and draws its nourishment from the living cells. The spores are regarded as chlamydospores, that is to say, localized, thick-walled segments of the hyphæ having the properties of reproductive cells. These spores are met with in three forms in the Uredineæ. The

Teleutospores (from τελευτή, an end), which are the type most universally present, arise towards the end of the vegetative period. In the majority of cases they remain dormant during the winter. On germinating they form a 4-celled basidium, from each cell of which a conidium is abstricted. Commonly the teleutospores are in rows of two, *i.e.* constitute spindle-shaped, 2-celled bodies, each cell (spore) of which can produce a basidium. Sometimes the teleutospores are in many-celled rows, occasionally solitary. The *Uredospores* (from *uro*, to burn) as a rule precede the teleutospores and germinate at once. They are oval and unicellular. The *Æcidiospores* arise in chains in special receptacles (the æcidium-fruits) which are at first closed. Both uredospores and æcidiospores differ from teleutospores in that they produce a mycelium at once on germination. They never form basidia and conidia. A fourth sort of reproductive organ, a secondary conidial stage, is often found associated with the æcidium stage; this is the pycnidium (*cf.* p. 678), a hollow receptacle whose lining cells abstract tiny condia. The fate of these pycno-conidia and the part they play in the life-history of the Fungus is unknown.

There is thus in the Uredineæ great variety in the kinds of reproductive cells. Some species possess all of them and produce them one after another upon the same host-plant (e.g. *Puccinia galii* and *P. primulæ*); others possess teleutospores only or teleutospores and one of the other types, whilst in others again all the forms are present, but they are not developed upon the same host-plant. This latter property of developing the different stages on two host-plants (known as *heteræcism*) is by no means uncommon amongst the Uredineæ. It is remarkable enough to merit a short description here, though, of course, any exhaustive account of the family as a whole is impossible. The following are well-known cases of heterœcism. *Coleosporium senecionis*, which produces its uredospores and teleutospores on the Groundsel (*Senecio vulgaris*), its æcidiospores on *Pinus sylvestris* (the latter stage formerly known as *Peridermium pini*); *Puccinia graminis*, which produces its uredospores and teleutospores on Wheat and other grasses, its æcidiospores on the Barberry (this stage formerly known as *Æcidium berberidis*); *Gymnosporangium juniperinum*, which produces its teleutospores on the Juniper, its æcidiospores on the Mountain Ash (*Pyrus aucuparia*). These three may serve as types of a very large number of similar forms. *Puccinia graminis*, the Rust of Wheat, is the most famous of all. The æcidium-stage (accompanied by pycnidia) arises in spring on the foliage of the Barberry and the æcidiospores here produced cannot germinate on the same host, but only on Wheat, Oats, Rye, or some other Grass. Here a new mycelium is established bearing first uredospores and later on teleutospores. The uredospores can germinate at once on other grasses, but the teleutospores remain dormant through the winter, and in spring give rise to basidia from which conidia are abstricted; these conidia can germinate only on the Barberry—not on grasses—and from the mycelium which arises from them fresh æcidium-fruits are developed. In the absence of either host-plant (*i.e.* of the Barberry or of suitable Grasses) the life cycle of the *Puccinia* is of course interrupted. For the extermination of the Rust disease of cereals the removal of Barberry bushes is an obvious measure. In

parts of Europe, however (*e.g.* many upland valleys in Switzerland) this precaution is not taken and the *Æcidium*-covered Barberries and rusted crops may be seen standing side by side. It is true the rust does not destroy the wheat crop entirely but it seriously diminishes the yield of grain. Long before the life-history of the Rust-fungus had been scientifically traced the Barberry was known to have an evil influence upon cereals. So long ago as 1760 the state legislature of Massachusetts passed an Act[1] compelling the inhabitants to extirpate all Barberry bushes. The main facts connected with the life-history of *Gymnosporangium* have already been mentioned (*cf.* p. 522), and the two stages are represented on p. 521. The projecting lobes on the Juniper (fig. 357 [1], page 521) consist of masses of teleutospores embedded in mucilage. When wetted they swell up, the basidia are produced and the conidia abstricted; the latter are then blown away and, should they alight upon the young foliage of a suitable member of the Pomaceæ, penetrate the tissues and produce the *Æcidium* stage. The effects of various other members of this group are referred to on pp. 524, 525. Between four and five hundred parasitic Uredineæ have been distinguished.

Auriculariaceæ. — Include the well-known Jew's-ear Fungus (*Auricularia sambucina*) not infrequent on dead branches of the Elder. From its fertile surface basidia with conidia resembling those of the last family are produced, but the basidia are continuous with the hyphæ of the Fungus, no chlamydospores being produced

Tremellaceæ.—Gelatinous forms found on rotting tree-trunks. Their substance is curiously lobed and plaited; *Tremella Mesenterica*, which forms large gelatinous orange masses on dead branches, is the commonest of them.

Pilacraceæ.—Include a single genus only, *Pilacre*; it grows on Beech-bark, and consists of a spherical head mounted on a stalk. It is of interest because its basidia (from which the conidia are abstricted) are inclosed in a loose layer of hyphæ—the outward continuations of the hyphæ upon which the basidia are borne—and it is thought to lead towards the family of the Gasteromycetes, in which the basidia are entirely covered in.

Dacromycetes.—Gelatinous forms resembling the Tremellaceæ. They approach the Hymenomycetes in that their basidia are destitute of septa. The processes from which the conidia are abstricted are very long. *Dacromyces deliquescens* is common as a red-coloured tough gelatinous mass on wooden palings.

Hymenomycetes.—An extensive family characterized by the production of a

[1] THE BARBERRY LAW OF MASSACHUSETTS.—Anno Regni Regis Georgii II. Vicesimo Octavo, Chap. X. (published January 13, 1755).

An Act to prevent Damage to English Grain arising from Barberry Bushes.

Whereas it has been found by experience, that the Blasting of Wheat and other English grain is often occasioned by Barberry Bushes, to the great loss and damage of the inhabitants of the Province:—

Be it therefore enacted by the Governour, Council, and House of Representatives, that whoever, whether community or private person, hath any Barberry Bushes standing or growing in his or their Land, within any of the Towns in this Province, he or they shall cause the same to be extirpated or destroyed on or before the thirteenth Day of June, Anno Domini One Thousand Seven Hundred and Sixty. And so forth. (From Plowright's *British Uredineæ.*)

fertile surface (the *hymenium*) consisting of basidia with 4 processes (or *sterigmata*) from each of which a conidium (or *basidiospore*) is abstricted. Typical basidia are represented in fig. 389[2], p. 684, and fig. 390[5]. The hymenium in this group is exposed at the time when the basidiospores are produced.

As in the Ascomycetes, so here, there is an extensive range of forms from simple to complex. Simplest of all are the *Exobasideæ*, mostly parasites on Ericaceæ. *Exobasidium Rhododendri*, which causes the Alpine Rose apples, has already been mentioned (p. 520), as also *E. Vaccinii* and *E. Lauri* (p. 526). The hymenium in these simple forms is produced over the whole surface of the hypertrophy or blister caused by the Fungus. In the *Telephoreæ* a definite tissue bearing the hymenium is developed; this is termed the hymenophore or fructification. In the simple *Corticium* this forms smooth sheets of waxy nature everywhere encrusting the substratum. The basidia occur over the free surface. *Stereum*, also very common on old trunks, forms leathery plates usually attached laterally or stalked. The hymenium is on the smooth under surface, whilst the upper surface of the fructification is more or less velvety. *Craterellus* (fig. 390[7]), laterally attached, is hollowed out above; the under surface is the fertile one. In the *Clavariæ* the fructification is club-shaped and fleshy, and covered externally by the hymenium—as in the sulphur-yellow *Clavaria inæqualis* very common on grass lawns and pastures—or it is branched and coral-like as in *Clavaria aurea* (fig. 390[1]). In the *Hydneæ* there is a well-marked distinction into a stalk and cap (known as the *pileus*); the hymenium is on the under surface, and is in the form of a number of crowded spines or teeth (e.g. *Hydnum imbricatum*, fig. 390[8]). The *Polyporeæ* form a large and important group, characterized by the fact that the hymenium has the form of a number of pits, tubes, or meshes, usually on the under surface of the fructification. The simplest of these is the Dry-rot Fungus, *Merulius lacrymans*. The mycelium of this Fungus penetrates the substance of ill-preserved woodwork in houses, disintegrating it and reducing it to a brittle consistency. At places it produces fructifications, flat irregular bodies whose under surface, the hymenium, consists of a honeycombing of shallow depressions. The property which these fructifications possess of excreting drops of water has given to this Fungus the name *lacrymans*. In *Polyporus* the hymenium has the form of numerous fine tubes lined with basidia. The fructification may be either bracket-like, as in *Polyporus fomentarius*, or it may have the cap-like form of a mushroom mounted on a central stalk, e.g. *P. perennis* (fig. 390[9]) and the allied *Boletus edulis*; in both the cases cited the hymenial surface is, of course, directed towards the ground. To these Polyporuses belong some of the most destructive diseases of timber, their myceliums penetrating the wood everywhere, softening and disintegrating it (e.g. *Polyporus igniarius*, *P. fomentarius*, *P. sulphureus*, and *P. annosus*—otherwise known as *Trametes radiciperda*). The last-named *P. annosus* causes a well-known disease of coniferous timber, the wood coming out in white spots before it is finally disintegrated. It is of interest because the fructifications are produced on the roots of the trees attacked. Allied to *Polyporus*

is *Dædalia* (fig. 390 [2]) a bracket-like form in which the hymenium takes the form of irregular branching slits on the under surface. The *Agaricineæ*, which include the very numerous mushroom and toadstool Fungi, are for the most part umbrella-like in form, having a central stalk and expanded circular receptacle (the pileus). The under surface of the pileus is occupied by lamellæ or gills which radiate from the insertion of the stalk to the margin of the pileus (*cf.* figs. 390 [3, 4, 6]). The basidia forming the hymenium are set upon the sides of these gills. Fig. 389 [1] shows an enlarged section through a part of a gill. In the more complex forms certain structures are present inclosing the young fructification, but they are ruptured as the pileus expands, and in adult fructifications the gills are freely exposed. Their remains may often be seen on the mature Fungus, as in *Amanita* (fig. 390 [6]). Just below the pileus there is a membranous ring (the *annulus*); at an earlier period it was attached to the margin of the pileus covering in the hymenium, and forming what is termed the *velum partiale*. In the same Fungus may be noted the remains of another sheath, the *velum universale*, which enwrapped the entire fructification. This is shown in fig. 390 [6] as a ruptured sheath (the *volva*) at the base of the stalk, whilst portions of the covering which invested the pileus (and was continuous with the ruptured sheath alluded to) are to be seen as white felty patches on the top of the scarlet pileus of *Agaricus muscarius*. The forms and varieties of the Agaricineæ are far too numerous even for mention. Many of them are edible, notably the Mushroom, *Agaricus campestris*, *Pholiota mutabilis*, and the yellow-coloured *Cantharellus cibarius* (allied to the Agaricineæ). Others again are poisonous, as, for instance, the scarlet *Agaricus muscarius* just cited, which receives the name *muscarius* from the fact that decoctions of this Fungus were formerly used for killing flies. Certain forms (*Russula* and *Lactarius*) contain a latex of a white or yellow colour. A number are characterized by producing sclerotium-like bodies (*cf.* p. 681). As a rule in the Agarics the fructifications arise directly from the mycelium, but in *Coprinus stercorarius*, *Lentinus*, &c., tuber-like masses of fungal substance are formed, and it is from these that the fructifications arise. These sclerotia, often attaining large dimensions, have been found by travellers in various parts of the world, and the fructification which arises from them is not in all cases known. Several of them, formerly name *Pachyma*, &c., are now known as belonging to the genus *Lentinus*. Very curious are the string-like sclerotia of *Agaricus melleus* which, from their root-like nature, were formerly termed "Rhizomorphs". They are found especially in Conifers, growing between the wood and bark, and having a ribbon-like form; from them cylindrical branches may arise which penetrate the soil and attack the root of some other tree. Ultimately the mushroom-like fructifications arise from these rhizomorphs.

A few lichens derived from the Hymenomycetes are treated at p. 695.

Gasteromycetes.—These are characterized by the fact that the basidia arise in closed chambers, which collectively constitute the *gleba*, and that this is covered by a continuous cortex or *peridium*. They include the Puff-balls, Earth-stars, Stink-

horns, &c. They are all of them more or less subterranean saprophytes, appearing above the surface to discharge their spores. The arrangements for the accomplishment of this purpose are very varied. The Puff-balls include the genera *Lycoperdon, Bovista, Scleroderma*, &c. When young a large portion of the interior has a chambered structure (the gleba), and in these chambers the spores are budded off. At maturity the fructification appears above the surface of the ground, and the whole of the substance of the walls of the chambers breaks down, except for certain branching threads (the *capillitium*, see fig. 391 [3]), which persists along with the

Fig. 391.—Gasteromycetes.

[1] *Lycoperdon constellatum.* [2] *Tulostoma mammosum.* [3] Capillitium and spores of *Tulostoma.* [4] *Geaster multifidus.* [5] *Geaster fornicatus.* [6] *Cyathus striatus.* [7] Longitudinal section of same. [8] *Clathrus cancellatus.* [3] ×80; [7] slightly enlarged; the rest nat. size.

minute spores (*Scleroderma* has no capillitium). The latter escape by the peridium becoming perforated. *Lycoperdon* (see fig. 391 [1]) differs from *Bovista* in having a sterile basal portion, which is sometimes considerably elongated. In *Tulostoma* (fig. 391 [2]) the outer layer of the peridium bursts and the sterile basal portion elongates considerably, hoisting up the gleba inclosed in an inner peridium. The Giant Puff-ball (*Lycoperdon giganteum*) sometimes attains huge dimensions—occasionally a metre in diameter. Allied to the Puff-balls is *Geaster*, the Earth-star (figs. 391 [4] and 391 [5]). In this genus the outer peridium splits into segments and folds back, the inner peridium becoming perforated and liberating the spores. Earth-stars are met with now and then, but they are not usually very common. In *Cyathus* (figs. 391 [6] and 391 [7]) we have a form resembling a little bird's-nest

containing eggs. Here the chambers, instead of being numerous and deliquescent as in *Lycoperdon*, are few and provided with thick, hard walls; they arise in a matrix which occupies the whole body of the Fungus, and when mature they become isolated by the disappearance of the matrix. Each chamber is attached by a string to the wall of the peridium (*cf.* fig. 391 [7]). The opening at the top arises by the coming away of a membrane which previously closes it in. Perhaps the most remarkable group of Gasteromycetes is the *Phalloideæ*, which includes the common Stink-horn Fungus and other forms. Whilst immature they are egg-like, but at ripening the investment bursts and the remarkable gleba is hoisted up. *Clathrus* (shown in fig. 391 [8]) has its gleba spread over a hollow spherical lattice-work; the gleba is red in colour and the appearance of the Fungus very striking; it is rare in this country. The Stink-horn, *Phallus impudicus*, is less rare. When the gelatinous investment bursts, a spongy, spindle-shaped stalk expands and raises up the green, cap-like gleba. The Phalloideæ depend upon insects for the dispersal of their spores. Flies are attracted by the bright coloration and foul smell of these Fungi, and they lick up the mucilage into which the gleba deliquesces with great avidity. Perhaps the tropical *Dictyophora phalloidea* is the most remarkable of the group. It resembles a *Phallus*, but unfolds around itself a delicate white network which hangs expanded from below the gleba-cap like a crinoline. It is thought that this appendage—like the white corolla of a night-flowering plant—renders the Fungus additionally conspicuous after dark. The Phalloideæ, in reference to their marked attraction for insects, are sometimes spoken of as the "Flowering Fungi".

ADDITIONAL GROUP OF FUNGI.

LICHENES.

In our review of the various alliances and families of Fungi the fact has been from time to time noted that certain members of various groups live symbiotically with Algæ as Lichens. Though obviously all these Lichen-fungi do not constitute a natural group or alliance, we propose treating them for convenience together. The general characters of Lichens and their mode of life have been already indicated in the chapter commencing at vol. i. p. 243; consequently little but an enumeration of the groups of Lichens and their methods of reproduction is required now. Briefly, a Lichen consists of a Fungus and an Alga upon which the Fungus lives parasitically. But it is something more than a mere parasitic Fungus on a green plant. The mycelium involves the Alga in the most complete manner (*cf.* fig. 392), but it doesn't kill it like an ordinary parasite. It lives upon the organic food which the Alga is able to manufacture in virtue of its chlorophyll, but without obvious injury to the Alga. Indeed, the algal cells often attain to a larger size and greater brilliance of colour than when growing freely. On the other hand, the Alga is nowhere in contact with the substratum (being inclosed in the substance of the Fungus), so that water

and dissolved salts are absorbed and supplied it by the Fungus. It is also protected by the Fungus, and able to exist in places where it could not live alone. Thus, for the Lichen, we speak of *symbiosis*, a living together. 'Tis true the Fungus is the predominant partner in this association, but it is not a parasite in the common acceptation of that term. Further, as predominant partner it is the Fungus which determines the form of growth and takes the initiative, the Alga following after. But even to this rule an exception has been found, and very likely others exist. For where two organisms live together, as in the Lichen, it may well happen that conditions may exist under which the Fungus can only control the Alga with difficulty, and that the Alga, attempting as it were to escape, compels the Lichen-fungus to follow it, not to lead. This indeed seems to be the case in one of the forms of that most remarkable of all Lichens, *Cora pavonia*, to be referred to below.

The conception of the Lichen as a dual organism, compounded of Fungus and Alga, is of relatively modern origin. Its establishment is due to the researches of Schwendener, which date back some thirty years, and to those of Bornet, which shortly followed them. Since those days the continued study of Lichens has tended only to secure for the "Schwendenerian theory" (as it was formerly termed) a more wide and universal recognition. Previous to the Schwendenerian epoch the Alga was regarded as a definite portion of the Lichen-thallus, its cells as arising from the hyphæ of the Fungus; indeed the Algæ were termed "lichen-gonidia". And for many years was the new view opposed by the majority of professed Lichenologists; but into this old controversy we have not space to enter here. It is sufficient to say that the Algæ of Lichens are referable to known genera and species of free-living Algæ, and that they have been determined for a number of cases. The Alga freed from the Lichen-fungus pursues its normal mode of life, and can then be identified; this is not always possible so long as it remains within the Lichen, owing to the change which the Fungus calls forth in it. It is a noteworthy fact that hitherto no Alga has been found so completely adapted to lichenism that it could not attain to its normal development outside the Lichen-thallus. On the other hand, Lichens have been raised from the spores of the Lichen-fungus allowed to germinate on free-growing Algæ. In this way a number of Lichens have been synthesized; and it has been shown that one and the same species of Alga could serve for several Lichens. Finally, the spores of Lichen-fungi have been grown on nutrient solutions, and have attained to advanced stages of development. In nature, however, with one exception (*Cora*, see below), it is not certainly known that any Lichen-fungus can grow independent of its Alga as substratum. We must regard the Lichen-fungi as being members of various Fungus-families which have become so specialized to a peculiar form of nutrition that under ordinary circumstances they do not develop upon anything except their Algæ. The Fungus-forms which occur in Lichens are vastly more numerous than are the Algæ; indeed the latter are drawn from relatively few families—from the Chroococcaceæ and and Nostoccaceæ of the Blue-green Algæ, and from the Protococcoideæ, Confervoideæ,

and Coleochæteæ of the class Gamophyceæ of Green Algæ. Thus the same Alga serves for many different Lichens.

Classifying Lichens according to the characters of the fungal constituent, we find members of the following families: Discomycetes, Pyrenomycetes, Hymenomycetes, and Gasteromycetes. We may therefore speak of 4 families of Lichens:

Discolichenes, Pyrenolichenes, Hymenolichenes, and *Gasterolichenes.*

Discolichenes.—All produce asci in apothecia after the manner of Discomycetes (*cf.* p. 682). The apothecia arise in numbers on the surface of the Lichen-thallus (*cf.* figs. 393 [2], 394, and 387 [2]), and the spores are formed in the asci in the usual way. In many genera the spores are multicellular. In not a few cases there are arrangements for the simultaneous distribution of the Alga-cells along with the

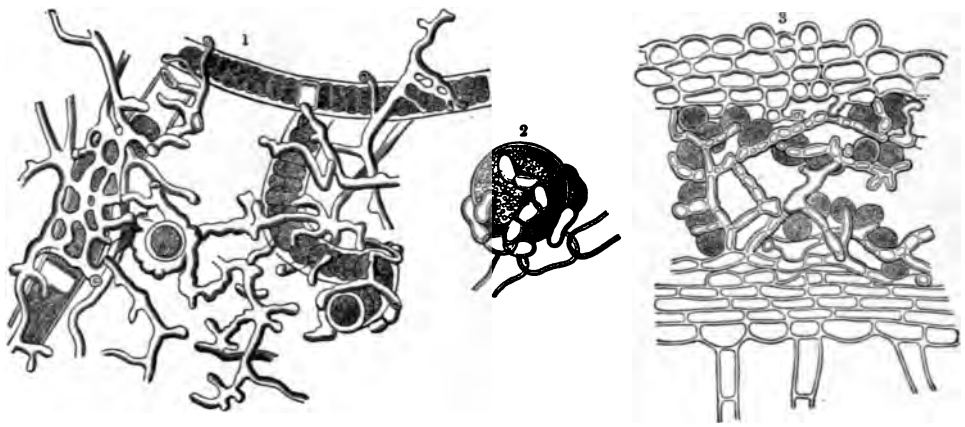


Fig. 392.—Lichens.

[1] Hyphæ of *Stereocaulon ramulosum* enveloping filaments of the blue-green Alga *Scytonema*; ×650. [2] *Cladonia furcata* with *Protococcus*; ×950. [3] *Coccocarpia molybdæa*, section of thallus; ×650. (After Bornet.)

ascospores, so that it shall not be left to chance for the spores to alight upon a suitable Alga. In these cases the algal cells bud actively below the layer of asci, and some are pushed up between the asci at the time when the latter reach maturity. Many Lichens possess also conidial fructifications, known as pycnidia (*cf.* p. 678). These are flask-like excavations, into which tiny conidia are budded by the lining cells. These receptacles were formerly termed spermogonia and the conidia spermatia; but the evidence that they have any such function as the terminology suggests is of the most slender description. On the other hand, these conidia have been caused to germinate and produce characteristic Lichen-thalluses in a number of cases. Pycnidia may be easily seen in the Iceland Moss (*Cetraria islandica*); they occur one in each of the tiny teeth on the margins of the ribbon-like thallus. Very common is vegetative propagation by means of brood-bodies known as *soredia.* These arise as little buds below the surface, and consist of an algal cell or two and a weft of fungal hyphæ. Being formed in quantities together they burst through to the surface as a dust-like powder and constitute the "soredia-heaps". They are distributed by the wind or washed away by rain. Both constituents of the Lichen

being present, they readily grow into fresh Lichens. In the majority of Lichens the Algæ are arranged in a definite layer or stratum (*cf.* figs. 392 [3] and 387 [2]); rarely are they distributed through the whole thickness of the thallus, as in the Gelatinous Lichens (*Collema*, fig. 393 [3]). Apart from these Gelatinous Lichens, the Discolichenes may be divided, according to their form, into Crustaceous, Foliose, and Fruticose Lichens. Crustaceous Lichens include such as are everywhere attached to their substratum (stones, bark of trees, &c.) and cannot be removed without injury. As examples may be mentioned the Lecideas, many of the Lecanoras, &c. The Foliose Lichens are not thus firmly attached; the thallus forms a shield- or ribbon-like expansion, readily separable from its substratum, as, for instance, the well-known orange Lichen *Physcia parietina*, the green-hued *Peltigera canina*, with

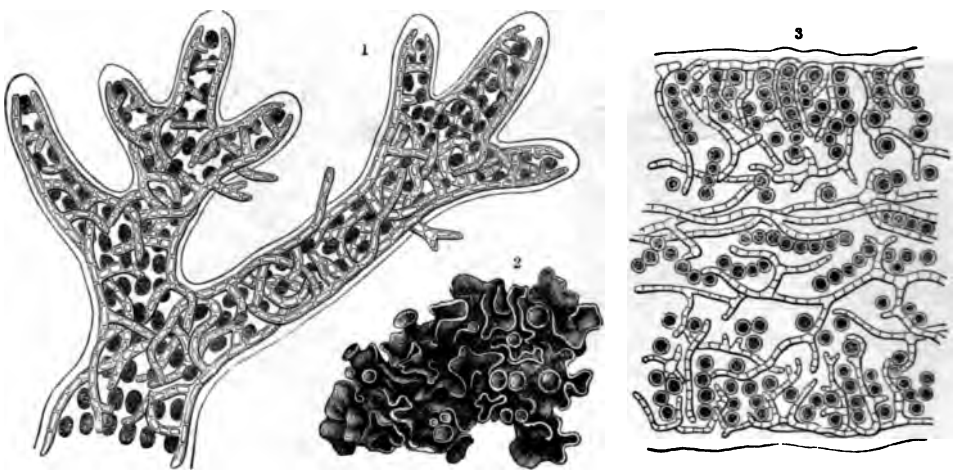


Fig. 393.—Gelatinous Lichens.

[1] *Ephebe Kerneri*; ×450. [2] *Collema pulposum*, nat. size. [3] Section of thallus of *Collema pulposum*, with *Nostoc* as Alga; ×450.

projecting umber apothecia, common in moist places amongst moss and stones, *Umbilicaria*, and many others. In the Fruticose Lichens the plant is only attached at one place, and has a shrub-like, branched appearance. Here are included many elegant and well-known forms, including *Usnea barbata*, the Old Man's Beard Lichen, which hangs in long tassels and festoons from the branches of trees, and sometimes produces large disc-like apothecia the size of sixpenny pieces. Another of these epiphytic forms is *Ramalina reticulata*, a Californian form which forms beautiful gray-green, ribbon-like nets. Nor must *Cetraria islandica*, the renowned Iceland Moss, and the Cladonias be omitted. The last-named are glaucous and generally erect-growing and branched. They include *Cladonia pyxidata*, the familiar Cup-moss, *C. rangiferina*, the Reindeer-Moss, and *C. coccifera*, growing on heaths with its scarlet, and *C. macilenta*, with orange apothecia, and several other species.

Pyrenolichenes.—In these the asci are contained in perithecia as in the Pyrenomycetes (*cf.* p. 678). Otherwise they are in general agreement with the last group, and include crustaceous, foliose, and fruticose forms. There are only a

few genera of Pyrenolichenes, including *Verrucaria*, *Ephebe*, *Endocarpon*, and *Sphærophorus*.

Basidiolichenes.—These occur only in tropical countries, and a number of genera were formerly distinguished, including *Cora*, *Dictyonema*, and *Laudatea*. *Cora pavonia*, the best-known form, consists of a greenish-yellow, fan-like, concentrically-striated thallus which produces its basidia on the under surface and contains *Chroococcus*-cells as its Alga; *Dictyonema*, on the other hand, consists of thin plates of rather felty consistency, in which the radiating character of the strands is very apparent; these delicate plates, blue-green in colour, stand out from the tree-branch to which they are attached. *Laudatea*, though resembling *Dictyonema*, is a crustaceous form. Both the latter forms have *Scytonema*-filaments as Algæ. Quite

Fig. 394.—*Lecanora esculenta*.

recently it has been shown by A. Möller, a naturalist who resided several years in Brazil, that all these supposed distinct Lichens are different growth-forms of one and the same Lichen. In addition to finding each of these forms in connection with the other—so that there is no doubt of their continuity—he found attached to the *Cora*-form the Fungus growing free from all trace of the Alga; this Fungus is one of the Telephoreæ (*cf.* p. 688), and when it is supplied with *Chroococcus*-cells grows into the *Cora*-form. This seems to be the only well-ascertained instance in which a Lichen-fungus has been found growing wild independent of an Alga. The *Dictyonema*- and *Laudatea*-forms consist of the same Fungus growing upon *Scytonema* instead of *Chroococcus*. In the *Laudatea*-form the Alga seems to get the upper hand and to determine the growth of the thallus. *Cora* and its various growth-forms is certainly the most interesting, as it is also the most beautiful of all Lichens of which we have any knowledge.

Gasterolichenes.—A Lichen from the Gasteromycetes has also been recognized; it is a little, shortly-stalked, puff-ball-like form resembling a *Lycoperdon* (*cf.* p. 690). The Alga (a *Palmella*) is restricted to the peripheral portions of the Lichen, which is named *Emericella variecolor*.

PHYLUM 3.—ARCHEGONIATÆ.

Plants showing a well-marked alternation of generations, that is of a sexual (oophyte) and an asexual generation (sporophyte). The latter reproduces the former by means of spores, the former the latter by means of egg-cells contained in archegonia. Fertilization is by means of spermatozoids which swim in water.

Class I.—BRYOPHYTA.

The sexual generation is in the greater number of cases a leafy shoot, arising from a branched, filamentous protonema. The asexual generation, which arises from the archegonium, is a stalked or sessile capsule containing spores; it is destitute of leaves, and never becomes independent of the oophyte.

Alliance XX.—Hepaticæ, Liverworts.

Oophyte nearly always dorsi-ventral; either thalloid or leafy. Protonema inconspicuous. Sporophyte a stalked or sessile capsule containing spores and usually elaters. A calyptra is not present.

Families: *Ricciaceæ*, *Marchantiaceæ*, *Anthocerotaceæ*, *Jungermanniaceæ*.

The oophyte generation in the first three families is a branched, ribbon-like, or lobed thallus (*cf.* fig. 196[1], p. 23), showing a distinction between its upper and lower surfaces, *i.e.* is dorsi-ventral. In the Jungermanniaceæ it is likewise thalloid in some forms, but in the great majority the oophyte has the form of a leafy shoot. The oophyte communicates with the substratum by means of rhizoids. The complete oophyte is preceded by an inconspicuous filamentous growth, the protonema, which arises directly from the spore, but this stage is not so well marked as in the Mosses. The sexual organs are borne usually in groups either in little depressions or upon special outgrowths of the thallus, or, in the leafy forms, are collected together into little "flowers" at the tips of the shoots or in the axils of the leaves. The female organs or archegonia are flask-shaped bodies with long necks, as in mosses. The egg-cell is contained in the enlarged basal portion, and on fertilization develops into the sporophyte or spore-capsule. The antheridia are delicate, stalked, oval or club-shaped bodies in which the 2-ciliate spermatozoids are developed. They resemble those of *Chara*, shown in fig. 374[7] (p. 660). The spore-capsule develops within the archegonium; its lower portion (in all but the simplest cases) forming a "foot" or sucker which remains imbedded in the substance of the oophyte, its upper portion forming the capsule proper. In many forms, particularly in the Jungermanniaceæ, a stalk is developed between foot and capsule, so that the latter is ultimately hoisted up. The capsule does not burst through the archegonial wall until the spores are ripe, nor is a portion of the archegonium raised up as a cap on the capsule as happens in the Mosses. The capsule ultimately opens by splitting into valves. In nearly all cases *elaters* are present with the spores. They are long thread-like cells with spiral thickening of the wall, and as they dry become very hygroscopic and

contractile. They assist in the dispersal of the dust-like spores in many cases, though the details of their co-operation in this respect is not always the same. Before the ripening of the spores the elaters play an important part in the nutrition of the spores; they are sterile cells or filaments intermixed with the spores to which they conduct food-substances during their development. Attention has been already drawn to the brood-bodies or thallidia of Liverworts (*cf.* p. 24).

Ricciaceæ.—These are very simple little forms occurring in wet places or floating in water (*Riccia natans*) like a Duckweed. The thallus is lobed or it may be ribbon-like and branched. The sexual organs are sunk in little chambers on the upper surface of the thallus; antheridia and archegonia may occur on the same or on different individuals. The fertilized egg-cell is here entirely converted into a spore-capsule, *i.e.* a sheath inclosing spores. No elaters are present in this family,

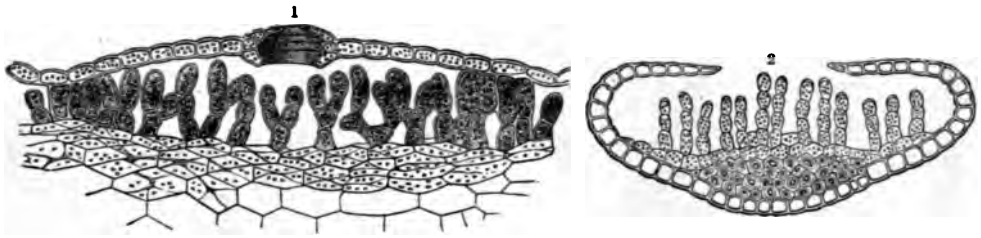


Fig. 395.

[1] Vertical section through an air-chamber of the Liverwort *Marchantia polymorpha* showing the stomate-like pore and the assimilating filaments. [2] Transverse section of a leaf of a Moss, *Barbula aloides*, showing the projecting plates of cells. [1] ×300; [2] ×330.

nor is there a sterile base or foot. The genus *Riccia* includes 107 species; there are 110 species in the whole family.

Marchantiaceæ.—The oophyte is a lobed band-like thallus (*cf.* fig. 196[1], p. 23) with marked dorsi-ventrality. On the upper surface are a number of chambers each opening to the exterior by a single stomate-like pore (*Marchantia*, fig. 395[1]). These chambers are really excavations of the upper surface which become closed in save for the pores in question. From the floor of each chamber sprout filaments of chlorophyll-containing cells (fig. 395[1]); these form the main assimilating tissue of the thallus. In *Marchantia* and *Lunularia* brood-bodies (or gemmæ) are budded off in cup-like receptacles (*cf.* fig. 196[1], p. 23). The sexual organs in this family are borne on special receptacles on the upper surface of the thallus. These may be either shield-like or stalked and umbrella-like (as in *Marchantia*, *Fegatella*, &c.). The male and female organs respectively occur on separate receptacles and are variously arranged. There are special sheathing structures associated with the archegonia. The sporophyte generation or sporogonium has a sterile base or foot which remains embedded in the archegonium. The spore-capsule is joined to the foot by a narrow, isthmus-like neck. The capsule opens by splitting into teeth. Elaters are present. Considerable variety is shown in this family in the form of the receptacles of the sexual organs.

165 species have been distinguished.

Anthocerotaceæ.—The oophyte has the form of a little lobed disc, in depressions of the surface of which the antheridia and archegonia are sunk. The sporogonium is long and cylindrical, and is invested in a circular sheath at its base. The spore-layer has the form of a hollow cylinder, leaving a sterile, central strand of tissue (the columella). Elaters are present amongst the spores, and serve as nutritive tissue for them rather than as instruments of dispersal. In this group

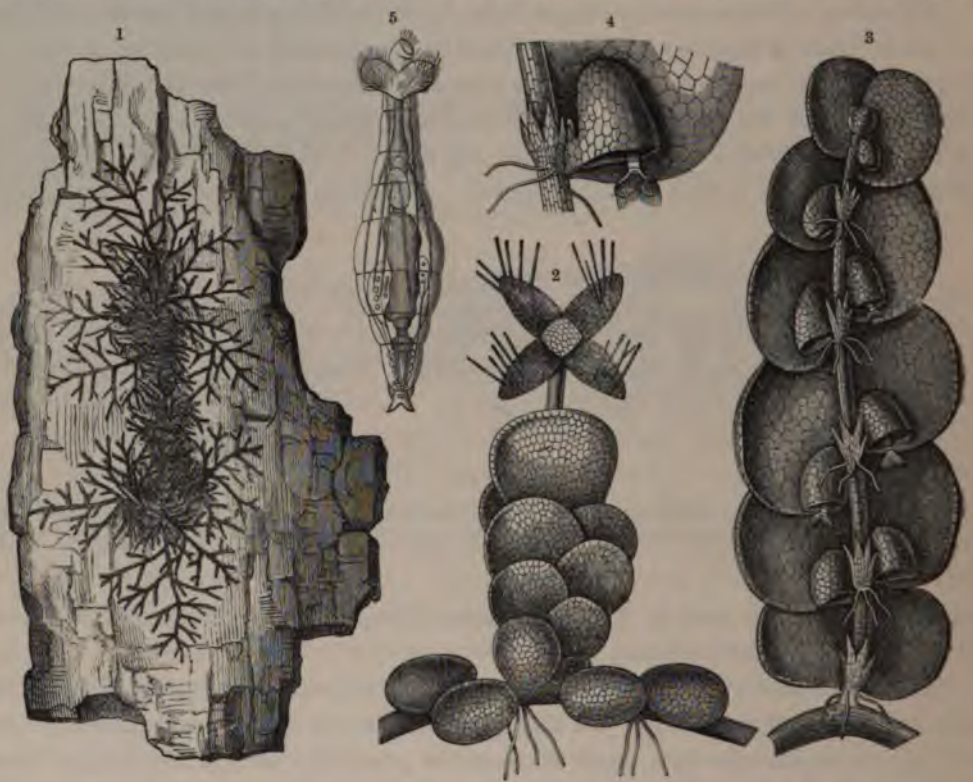


Fig. 396.—Jungermanniaceæ.

[1] *Frullania dilatata* growing on the bark of an Acer. [2] A small portion of this plant enlarged; it shows the stalked spore-capsule burst into four valves; attached to the valves are the elaters. [3] A shoot of the same *Frullania* seen from the under side; at the base of each leaf is a little pitcher containing a Rotifer. The little toothed scales lying on the stem are the amphigastria. [4] A single pitcher and its contained Rotifer [5] The Rotifer (*Callidina symbiotica*) removed from the pitcher. [1] nat. size; [2] ×20; [3] ×25; [4] ×30; [5] ×100.

—alone amongst the Liverworts—stomates occur upon the spore-capsule. It dehisces into two valves.

There are 103 species.

Jungermanniaceæ.—Include both thalloid forms, in which the oophyte generation has a general resemblance to that of a *Marchantia*, and creeping leafy forms (*cf.* fig. 396 [1]); the latter are by far the more numerous. The sporogonium in both cases consists of a long-stalked capsule which splits into four valves (fig. 396 [2]). Elaters are present, often attached to the capsule-wall. The Jungermanniaceæ grow for the most part on damp earth, stones, and bark of trees.

The thalloid forms include the very common *Pellia*—like a *Marchantia*, with

long-stalked capsules inserted on its thallus—*Metzgeria*, branched and ribbon-like, the curious aquatic *Riella* with its spiral membrane (see fig. 366, p. 611), and the rather complex *Symphyogyna* and *Pallavicinia* (chiefly tropical), with their creeping rhizomes and stalked fronds; these two forms, almost unique amongst the Liverworts, show a well-marked vascular system. The antheridia and archegonia are scattered over the surface of the thallus and not on stalked receptacles as in the Marchantiaceæ.

The *leafy* forms are very numerous and, as a rule, consist of branched axes which lie parallel to the substratum (e.g. *Frullania dilatata*, fig. 396 [1]). There are three rows of leaves, two towards the upper surface and one towards the lower. These ventral leaves, which are termed *amphigastria*, are tiny and scale-like (see fig. 396 [2]), and sometimes are only represented by hairs. The archegonia are usually borne in little groups at the tips of the main or lateral shoots, and are inclosed in involucres. The antheridia occur in various positions. The sporogonium is always a long-stalked capsule as in the thalloid forms. Not a few of the leafy Jungermanniaceæ produce curious little appendages or "auricles" at the bases of their leaves, and these are often developed into little pitchers (fig. 396 [3]). In other cases the amphigastria bear pitcher-like appendages of the same kind. These structures seem to be receptacles for the holding of water by capillarity against times of drought. In some forms Rotifers inhabit these pitchers (e.g. *Frullania dilatata*, figs. 396 [4] and 396 [5]), but there is no evidence to show that the Liverwort uses their bodies as food like ordinary pitcher-plants, or that any special relations exist between the Rotifers and the Liverwort. The pitchers are not gall-structures directly produced by the Rotifer—they develop equally well with or without them. They are probably formed by the plant simply for storing water, and are found by Rotifers and other small animals to be convenient abiding-places.

There are more than 3500 species of Jungermanniaceæ

Alliance XXI.—Musci, Mosses.

The oophyte generation is the leafy moss-plant; it arises as a lateral bud from the simple and generally filamentous protonema. The sporogonium has a seta and spore-capsule, the latter usually possessing a central sterile mass of tissue, the columella. The upper portion of the archegonium is often raised as a calyptra by the elongating sporogonium.

Families: *Sphagnaceæ*, *Andreæaceæ*, *Archidiaceæ*, *Bryaceæ*.

Sphagnaceæ.—These are the Bog-mosses, and they include a single genus, *Sphagnum*. The form of the protonema here depends on whether the spore germinates in water or upon a solid substratum; in the former case it is branched and filamentous, in the latter it is a cellular expansion, not unlike a fern-prothallium. The leafy moss-plant arises by budding from the protonema, and is remarkable on account of its water-retaining properties. The character of the leaves has been already described and figured at vol. i. p. 219. The sexual organs arise on special

shoots at the apex of the plant (fig. 397 [14]); these shoots are respectively male and female, and may occur on the same or on different plants. The antheridia are in the axils of the leaves of the male shoots, the archegonia in groups at the tips of the female shoots. The fertilized egg-cell develops into the sporogonium, the lower portion of which forms a large foot, whilst the upper part swells up into the spore-

Fig. 397.—Mosses.

[1] *Polytrichum commune*; the spore-capsule to the left is concealed by the cap (calyptra), that to the right is exposed. [2] The same moss in an earlier stage of development. [3] Spore-capsule of *Polytrichum commune* with its lid. [4] The same after the falling away of the lid. [5] *Bryum cæspiticium*. [6] Spore-capsule of same with its calyptra. [7] The same after removal of the calyptra. [8] The same after removal of the lid, showing the teeth (peristome). [9] A portion of the peristome, enlarged. [10] Antheridia, archegonia, and paraphyses of *Bryum cæspiticium*. [11] *Hylocomium splendens*. [12] Spore-capsule of same. [13] *Andreæa rupestris* with burst spore-capsule. [14] *Sphagnum cymbifolium*; the spore-capsules are still intact in the left-hand specimen. [15] A single capsule of the same. 1, 2, 5, 11, 14, natural size; 3, 4, 6, 7, 8, 12, 13, 15 ×5; 9, 10 × 150.

capsule. The spore-layer in the latter has the form of a hemispherical shell. Ultimately the archegonium is burst irregularly by the enlarging sporogonium, and the spores are set free by the removal of a circular lid at the summit.

In *Sphagnum* a true seta is not developed, the region between foot and capsule remaining quite short. The same result, however, is achieved by a considerable

elongation of the axis of the female shoot taking place in the region immediately below the group of archegonia. The capsule is thus hoisted up on a long stalk, though this stalk is no part of the sporogonium (*cf.* fig. 397 [15]).

The remains of the Bog-mosses form an important constituent of peat.

Andreæaceæ.—A small family, including the single genus, *Andreæa*. They are amongst the first settlers upon new and inhospitable rock-surfaces, and play an important part as soil-formers (*cf.* vol. i. p. 266). In them the mode of bursting of the spore-capsule is altogether peculiar amongst Mosses. Four longitudinal slits

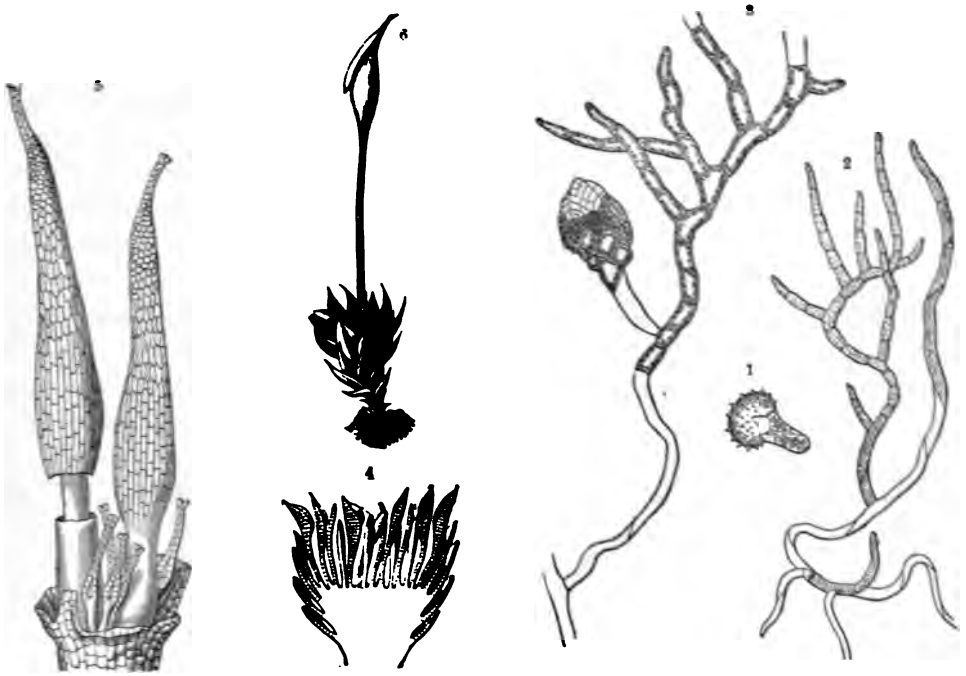


Fig. 398.—Mosses.

1 A germinating spore. 2 A Moss-protonema. 3 Protonema giving rise to a bud from which will arise a leafy moss-shoot. 4 Longitudinal section of the tip of a male shoot of a Moss; small, club-shaped antheridia are present between the scales. 5 Tip of a female shoot with archegonia; two of them containing sporogoniums have enlarged, and in the left-hand one of these two the upper part of the archegonium (calyptra) has been torn from the basal portion. 6 Leafy female shoot bearing a fully developed sporogonium; the calyptra is still in position. 1, 2, 3 × 350–400; 4 × 15; 5 × 80; 6 × 5.

arise in its wall, and the four valves remain attached to one another at the apex (*cf.* fig. 397 [13]).

Bryaceæ.—This family includes the vast majority of the Mosses. The germinating spore produces a simple, branching, filamentous protonema (figs. 398 [1] and 398 [2]) on the surface of the ground, certain of its branches developing as colourless rhizoids and penetrating the substratum. From the protonema the ordinary leafy Moss-plant arises as a lateral bud (*cf.* fig. 398 [3]). The curious properties of the protonema of the Luminous Moss (*Schistostega osmundacea*) have been already described (*cf.* vol. i. p. 385, and fig. 25A, *p*). The leafy shoots become rooted by the development of rhizoids from their lower extremities, and bear their leaves, as a rule, in three rows, though a slight twisting of the stem often disguises this fact.

The Luminous Moss just mentioned is an exception; in it the leaves are arranged in two rows (*cf.* fig. 399 [9]). The leaves of Mosses are generally simple, and (unlike the Jungermanniaceæ) provided with midribs. In many of the Polytricheæ, and in *Barbula aloides*, &c. (*cf.* fig. 395 [2]), the upper surface of the leaf bears longitudinal ridges of thin-walled chlorophyll-containing cells, thus adding to its assimilating and transpiring surface. The Moss-plant can propagate freely by means of brood-bodies and gemmæ. These sometimes take the form of modified leaves, sometimes of little stalked bodies on the leaves; occasionally they are collected together into little receptacles at the tips of the shoots, as in *Tetraphis* (*cf.* fig. 196, p. 23, where this and other cases are illustrated). The antheridia and archegonia are collected into little receptacles or "flowers" placed either at the tips of the shoots (in the *acrocarpous* Mosses, *cf.* figs. 397 [1] and 398 [6]), or laterally in the leaf-axils (in the *pleurocarpous* Mosses, *cf.* fig. 397 [11]). Occasionally both antheridia and archegonia are present together in the same "flower" (*cf.* fig. 397 [10]), but more frequently they are in separate receptacles (*cf.* figs. 398 [4] and 398 [5]). Mingled with them are sterile scales, the paraphyses. The structural details of the sexual organs and the mode of fertilization in Mosses has already been described (*cf.* pp. 64–66). After fertilization the egg-cell within the archegonium divides and enlarges, and gradually fashions itself into the sporogonium, the asexual generation of the Moss. For a time the archegonium stretches with the growing embryo, but sooner or later it is ruptured (*cf.* fig. 398 [5]), and its upper portion raised aloft on the sporogonium as the calyptra. Sometimes the calyptra forms a closely-fitting cap, entirely investing the capsule as in *Polytrichum* (fig. 397 [1]), or it may be a little hood split down one side as in *Bryum* (figs. 397 [6] and 398 [6]). After the raising of the calyptra by the elongation of the stalk or seta of the sporogonium the apex swells and develops into the capsule. Though in almost all cases the sporogonium consists of a capsule borne on a long smooth stalk (the seta), which is embedded below in the tissues of the female shoot of the Moss-plant, a very considerable amount of variety is met with in the structural details of the capsule itself. The seta may pass gradually into the capsule as in *Bryum* (fig. 397 [6]), or there may be a bulb-like enlargement (apophysis) at the base of the capsule as in *Polytrichum* (fig. 397 [3]), or this enlargement may attain considerable dimensions, exceeding the spore-producing part of the capsule, as in *Splachnum* (fig. 399). This apophysis is of importance as an assimilating and transpiring organ, and it is the only portion of the whole Moss which bears stomata. Within the capsule is the spore-layer. This has the form of a hollow cylinder surrounding a central sterile tissue, the columella. External to the spore-layer, and between it and the wall of the capsule, is a lacuna generally traversed by chlorophyll-containing filaments of cells. Above the spore-layer the columella expands into a mass of tissue, which forms the lid of the capsule (operculum, *cf.* figs. 397 [3] and 397 [7]). At the periphery of the lid, where it abuts upon the wall of capsule, a ring of cells becomes marked out (the annulus); later, by the rupture of this ring the lid comes away, and the mouth of the capsule is guarded only by a set of teeth, the peristome (*cf.* figs. 397 [8], 397 [9], 399 [3], and 399 [8]). By the time that the lid is ready to come

away the spores are ripe, and the columella, &c., have dried up and collapsed. The teeth of the peristome are exceedingly varied in pattern in the various genera of Mosses; typically there are two series of them forming an outer and an inner peristome (*cf.* fig. 397 [9]), but they are differently thickened, fused, and divided, and one or even both series (e.g. *Gymnostomum*), may be absent. They are very hygroscopic, and their function will be alluded to later on when we are discussing the

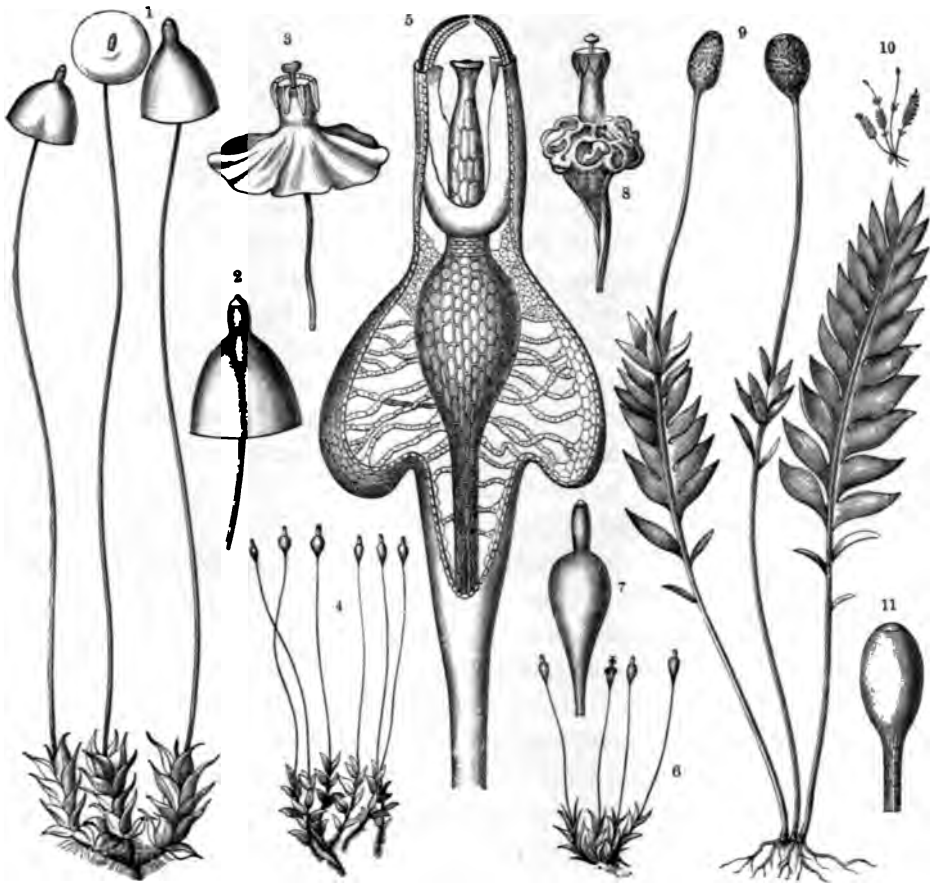


Fig. 399.—Spore-capsules of Mosses.

[1] *Splachnum luteum.* [2] An unripe capsule of the same. [3] A ripe and open capsule of the same. [4] *Splachnum vasculosum.* [5] Longitudinal section of a ripe capsule of this moss, showing the large apophysis below containing lacunæ, and traversed in the middle by the columella; above is the capsule proper with persistent columella, spore-sac, and peristome. [6] *Splachnum ampullaceum.* [7] An unripe capsule. [8] A ripe capsule of the same. [9] and [10] *Schistostega osmundacea.* [11] A ripe capsule of the same. 1, 4, 6, 10 natural size; 2, 3 × 2; 7, 8, 9 × 10; 11 × 15; 5 × 100.

distribution of spores. In the Polytrichæ the peristome is not quite the same as in other Mosses. In this group the teeth are very numerous and quite short, and from their apices a membrane (the epiphragm) remains stretched after the fall of the lid (*cf.* fig. 397 [4]). The spores here tumble out between the teeth.

The position of the sporogonium is of course determined by that of the female "flowers"; where these are terminal the sporogonium will be terminal (acrocarpous), similarly where lateral (pleurocarpous). The number of genera of Bryaceæ is so

numerous that it is hardly possible to mention even the most notable here. *Fontinalis* is of interest in being aquatic; *Splachnum* (*cf.* fig. 399) in having a very large apophysis and being saprophytic on animal excreta (*cf.* vol. i. p. 118). *Buxbaumia aphylla* is an exceedingly simple form and vegetates in the protonema-stage. Leafy shoots are only formed in connection with sexual reproduction, and even then they are very rudimentary. This plant has been thought to be a primitive type of Moss.

Fossil Mosses are met with in Tertiary and more recent deposits.

Class II.—PTERIDOPHYTA, Vascular Cryptogams.

As in the Bryophyta, so here, a well-marked alternation of generations is exhibited in the life-history. Whilst in the Liverworts and Mosses the oophyte is the dominant stage ("the plant") here the sporophyte constitutes "the plant". The oophyte is a mere prothallium of simple nature, the sporophyte is a complex structure with root, stem, and leaves, and a well-marked vascular system. It becomes free from the prothallium at an early stage in development. The Pteridophyta contain the following alliances: *Filices, Hydropterides, Equisetales, Lycopodiales.*

The plant or sporophyte generation attains to a wide diversity of form in the Pteridophytes; thus, amongst the Ferns the stem is often short and bears a rosette of fronds, or is elongated and rhizome-like with leaves at intervals; in the Equisetales it is erect and jointed, and the leaves are reduced to toothed sheaths; and in many Lycopodiales the stem is procumbent, much-branched, and covered with simple scale-like leaves over the entire surface. Upon the leaves are borne the sporangia which contain the spores. The sporangia may be either scattered over ordinary leaves or on special leaves collected into cones. There is one feature connected with the spores that must be described here. Though in the Ferns and in many other Pteridophytes all the spores are of one kind and each gives rise to a prothallium bearing both archegonia and antheridia, there are Pteridophytes in the alliances Hydropterides and Lycopodiales in which two sorts of spores are produced. The latter are known as heterosporous, the former as homosporous. Where the plants are heterosporous the spores are of two sizes, and the larger ones (macrospores) are contained in fewer numbers in the sporangia than are the smaller ones (microspores). On germination the macrospore gives rise to a female prothallium only, the microspore to a male prothallium; *i.e.* growths which bear respectively archegonia and antheridia. The male prothallium is a very simple structure, and its part is played so soon as it has liberated its spermatozoids. The female prothallium having to nourish the young sporophyte for a while, until such time as it can live independently, is larger, and is usually well-provided with food-material.

Contrasting the Pteridophytes and Bryophytes, the Fern-plant corresponds to the sporogonium of the latter and the prothallium to the Moss-plant or Liverwort thallus. In the former the sporophyte, in the latter the oophyte generation is the more complex. But that a Fern-plant has been elaborated out of a Moss-sporogonium, or that the Fern-prothallium is a reduced or degraded Moss-plant, is exceed-

ingly improbable. It is more likely that the two groups have had a common origin, and have then developed along entirely different lines

Alliance XXII.—Filices, Ferns.

Families: *Hymenophyllaceæ, Polypodiaceæ, Cyatheaceæ, Gleicheniaceæ, Schizœaceæ, Marattiaceæ, Osmundaceæ, Ophioglossaceæ.*

With us for the most part Ferns have short underground stems bearing a rosette of leaves as in the Male Fern (*Aspidium Filix-mas*) and Hart's-Tongue Fern (*Scolopendrium vulgare*), or there may be an elongated horizontal underground rhizome, as the Bracken Fern (*Pteris aquilina*) and Polypody (*Polypodium vulgare*), the leaves being produced at intervals. In the tropics and sub-tropical regions, on the other hand, Tree Ferns are common. They belong mostly to the genera *Cyathea, Alsophila,* and *Dicksonia.* In these a considerable caudex is developed (*cf.* fig. 347, p. 473, and vol. i. p. 714), which is often enveloped in a perfect plexus of aërial roots. Many Ferns are epiphytic, especially in tropical forests (e.g. *Platycerium alcicorne,* fig. 349, p. 475); with us *Polypodium vulgare* is often met with enveloping the trunks and boughs of large trees. The tropical genus *Lygodium* is characterized by its climbing habit, the long rachis of its compound leaf twining like the stem of a twining plant. The view has been held, and is alluded to on p. 12, that the fronds of Ferns are not really leaves but modified stem-structures, the scaly structures that occur on the stem and fronds being regarded as the true leaves. It is sufficient to say that this view is not very widely held amongst Botanists, and that here the term leaf is used as synonymous with frond. Broadly speaking, Ferns love moist and shady habitats; they grow especially in woods and forests, and on humid rocks beside streams, &c. Generally their leaves are thin and delicate, and ill-adapted to withstand prolonged desiccation.

Borne on the leaves of Ferns are the sporangia, tiny capsules in which the spores are developed. The form of the sporangium and the arrangement of these bodies varies in the different families of Ferns—indeed the sporangia afford characters which are used for the grouping and classification of Ferns. In the commonest Ferns (belonging to the predominant family Polypodiaceæ) the sporangium resembles two watch-glasses placed together, the rim being occupied by a series of large, thick-walled cells (the annulus), and the whole mounted on a little stalk (*cf.* fig. 400 [14]). In other families the stalk may be absent, the annulus incomplete, oblique, transverse or altogether wanting, &c., as will be pointed out in treating the several families. The sporangia are aggregated into clusters, the sori, and these are in many cases protected by little outgrowths of the leaf-surface (indusia) or under the infolded margins of the leaf. The form and arrangement of the sori and indusia provide the characters according to which the large family Polypodiaceæ is subdivided.

Hymenophyllaceæ.—The Filmy and Bristle Ferns. There is generally a rhizome which bears delicate fronds at intervals (*cf.* fig. 400 [2]); the lamina of the

leaf is often only one cell thick, and stomata occur only in the genus *Loxsoma* (New Zealand). The other genera, *Hymenophyllum* (the Filmy Fern) and *Trichomanes*, are both met with in Great Britain. The former is not uncommon on the rocks beside waterfalls, but the latter (*Trichomanes radicans*, the Killarney Fern) seems to be almost restricted to the south of Ireland. In this family the sporangia occur at the margins of the fronds on the excurrent veins (see fig. 400 [3]). They are sessile, and the annulus is transverse, *i.e.* at right angles to the axis of the sporangium. The sorus is surrounded by an enclosure formed from the leaf-margin; this investment is cup-shaped in *Trichomanes* and bivalved in *Hymenophyllum*. Often in the former genus the axis on which the sporangia are inserted projects considerably from the cup—hence the name Bristle Fern. In this family the prothallium is unlike that of other ferns, being frequently filamentous and branched; the filaments often bear local expansions, upon which the archegonia are inserted.

There are about 200 species of Hymenophyllaceæ.

Polypodiaceæ.—By far the largest family of Ferns; indeed this family includes more than three times as many species as all the rest of the Pteridophytes together. Almost all our familiar European Ferns belong to it. The character which they all have in common is a stalked sporangium (fig. 400 [14]), with vertical annulus. The distribution and form of the sori are exceedingly various. The Polypodiaceæ have been separated into the following tribes:—*Pteridæ*, *Aspidieæ*, *Asplenieæ*, *Davallieæ*, *Polypodieæ*, *Grammitideæ*, *Acrostichæ*. In the *Pteridæ* the sori occur at the margin of the leaf; in the Bracken Fern (*Pteris aquilina*) the frond is much branched, and the sori are everywhere continuous on the pinnule-margin; they are covered in by an indusium derived from the margin; in the Maiden-hair Fern (*Adiantum Capillus-Veneris*) the tip of the pinnule is folded back over the sorus. In the *Aspidieæ* the sori are scattered, circular, and covered in by a circular or kidney-shaped indusium. *Aspidium Filix-mas* (the Male Fern) belongs to this tribe. The sorus is much elongated and linear in the *Asplenieæ*, and the indusium is inserted on one side of it (e.g. *Asplenium Ruta-muraria*, figs. 401 [6] and 401 [7]). The Lady Fern (*Athyrium Filix-fœmina*), Hard Fern (*Blechnum*), Hart's-tongue (*Scolopendrium*), &c., are members of this tribe. In the *Davallieæ*, which include the large tropical genus *Davallia*, the sorus is near the margin, and inclosed in a pocket-like indusium. In the *Polypodieæ* the sori are circular and scattered over the under surface of the frond. There is no indusium (see fig. 400 [5]). The *Grammitideæ* resemble the last-named in the absence of an indusium. The sori usually follow the veins, frequently forming very elegant reticulations on the under surface of the leaf, as in the tropical genus *Hemionitis*. The Gold and Silver Ferns (*Gymnogramme*) belong to this tribe. In the *Acrostichæ* the whole under surface is covered with sporangia, and there is no indusium. Examples are, *Rhipidopteris* (fig. 400 [4]), *Platycerium* (fig. 349, p. 475), and *Acrostichum*.

Nearly 3000 species of Polypodiaceæ are known.

Cyatheaceæ.—This family includes the Tree-ferns (fig. 347, p. 473). The annulus of the sporangium is slightly oblique; it is only indifferently represented in

Fig. 400.—Various Ferns.

[1] *Nephrolepis Duft.* [2] *Trichomanes Lyallii.* [3] Sorus of the same fern, with cup-shaped investment seen in longitudinal section. [4] *Rhipidopteris peltata.* [5] *Polypodium serpens.* [6] Portion of frond of *Gleichenia alpina.* [7] *Schizæa fistulosa.* [8] *Botrychium lanceolatum.* [9] Under side of a fragment of the frond of *Gleichenia alpina*; above the sporangia are concealed by a tuft of scales, below they are exposed. [10] and [11] Fertile pinnule of *Cyathea elegans.* [12] Longitudinal section of a sorus of *Cyathea.* [13] Sporangium of *Cyathea.* [14] Sporangium of *Polypodium.* [15] Sporangium of *Schizæa.* [16] Under side of the prothallium of *Asplenium.* 1, 2, 4, 5, 6, 7, 8 natural size; 3, 9, 10, 11, 12, 13, 14, 15, 16 × 5–20.

fig. 400[13]. In *Cyathea* (figs. 400[10, 11, 12]) the indusium is cup-like, and closed until the spores are ripe. In *Dicksonia* the sorus is marginal, with bivalved indusium; in *Alsophila* the sori are scattered, and the indusium absent or rudimentary; in *Hemitelia* the indusium is scale-like, and situated on one side of the sorus. Of Cyatheaceæ about 200 species are known.

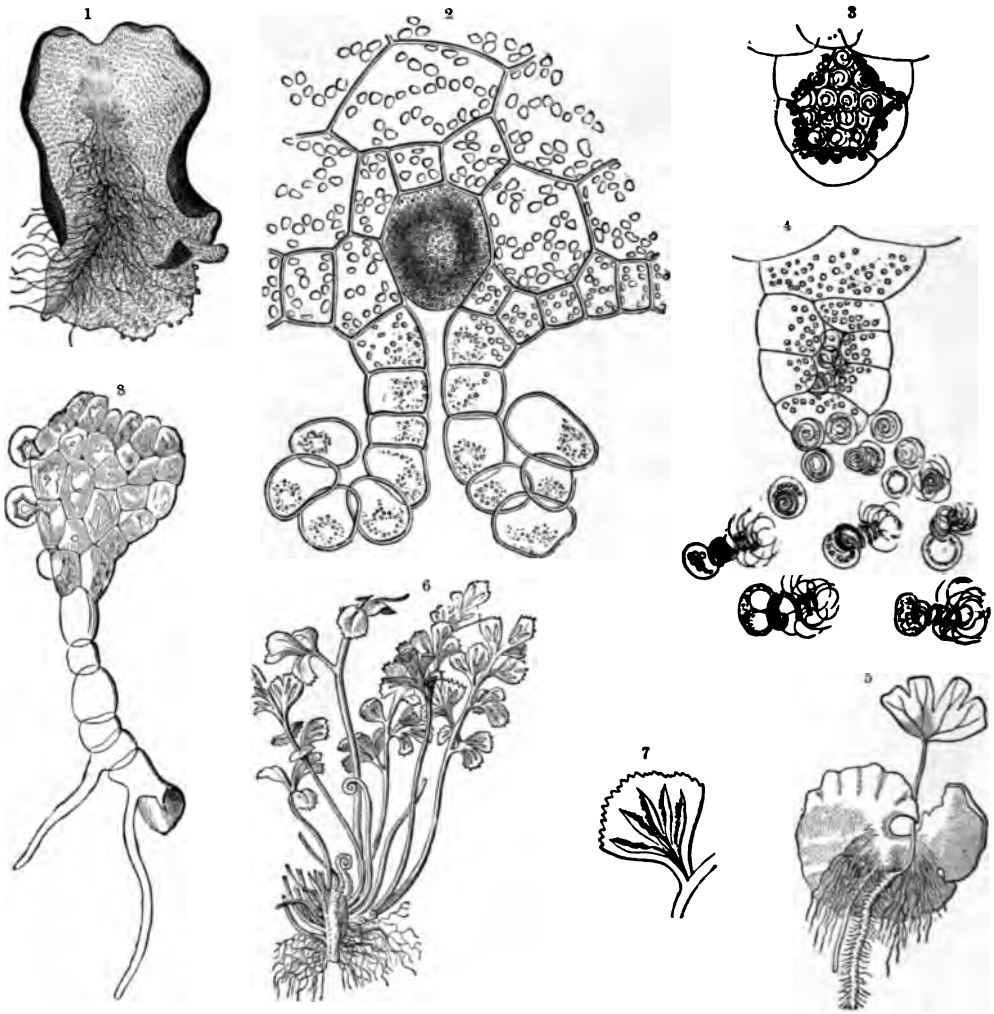


Fig. 401.—Life-history of a Fern.

[1] A Fern-prothallium seen from the under side. [2] An archegonium in longitudinal section. [3] An antheridium. [4] Escape of spermatozoids from antheridium. [5] Young sporophyte with first leaf arising from the prothallium. [6] Complete sporophyte of *Asplenium Ruta-muraria*. [7] Under surface of pinnule of same, showing linear sori and lateral indusia. [8] A young prothallium arising from a spore; the spore is below. [6] natural size; [1] × 8; [2], [3], [4] × 350; [5] × 6; [7] × 3; [8] × 240.

Gleicheniaceæ.—Mostly tropical forms. The sporangia have a transverse annulus, and are collected into little sori of 3 or 4 sporangia, often very closely packed (*cf.* figs. 400[6], and 400[9]). The frond usually forks repeatedly. There is only one genus, *Gleichenia*, which has some 40 species.

Schizæaceæ.—The members of this family are also for the most part tropical.

The sporangium is sessile, and the annulus is situated at the apex like a cap (*cf.* fig. 400 [15]). In *Schizæa* (fig. 400 [7]) the fertile pinnules bear two rows of sporangia partly sunk in little pockets; in the climbing fern *Lygodium* the leaflets bear little fertile spikes at the margin, and the sporangia are sunk completely in little pockets, one row on either side of the spike. In *Aneimia* the frond divides into two portions—a green vegetative portion, and several fertile branches whose ultimate ramifications are beset with naked sporangia. In habit *Aneimia* is not unlike a *Botrychium* (*cf.* fig. 400 [8]). Of Schizæaceae there are some 70 species.

Marattiaceæ.—Tropical Ferns, many of them attaining considerable dimensions. The fronds are distinguished by possessing a pair of stipules at their base. The sporangia are more bulky than in the families hitherto enumerated, and in *Angiopteris* are arranged in rows very close together, whilst in *Marattia, Kaulfussia,* &c., all the sporangia of each sorus are joined together into little button or bean-like bodies. There is no distinct annulus, though a little cap of cells possibly represents one. There are 25 existing species, but this family was much more abundant, than it now is, in palæozoic times; their remains are abundant in the Coal Measures.

Osmundaceæ.—Here also the sporangium is destitute of annulus, and possesses a little cap of cells in place of it. In *Osmunda regalis,* the Royal Fern, the upper pinnules of the frond alone produce sporangia, but in such quantity that their whole surface is covered with them; thus the tips stand out in marked contrast to the rest of the frond (hence the name "Flowering Fern"). The other genus of the family, *Todea,* resembles a Filmy Fern in the delicate texture of its leaves. There are only 11 species altogether.

Ophioglossaceæ.—A small family including the Adder's-tongue (*Ophioglossum*) and Moonwort (*Botrychium*). The frond here divides into a sterile and a fertile portion, the latter seeming to arise from the base of the former. In the Adder's-tongue the sterile portion is unlobed, and the fertile portion spicate, the sporangia being sunk in its substance. In the Moonwort (*cf.* fig. 400 [8]) both parts are branched, the fertile portion resembling a panicle. The prothallium in this family is a little subterranean tuberous body. The origin from it of the sporophyte generation has not followed in any instance. There are twelve species of Ophioglossaceæ.

Alliance XXIII.—Hydropterides, Rhizocarps.

This alliance is nearly associated with the Filices and more particularly with the earlier rather than with the last-mentioned families of that alliance. All the genera are more or less aquatic in habit; but their distinctive feature is the fact that they are *heterosporous, i.e.* that some sporangia contain macrospores (one in each sporangium) the others microspores. The sporangia are collected into sori, which are inclosed by metamorphosed leaf-segments into little fruit-like bodies.

Families: *Salviniaceæ, Marsiliaceæ.*

All the members of the alliance agree in their aquatic habit and in being heterosporous. The macrosporangia are larger than the microsporangia, and contain one

big oval macrospore; the microspores are produced in numbers in the microsporangia. The macrospore, in addition to a hard wall, possesses an external gelatinous layer with stratified structure. On germination, the macrospore develops its (female) prothallium at one end, and, on the bursting of the spore-wall at the apex, this prothallium and the archegonia developed on its surface, are exposed. Of the contents of the spore, only a portion forms the prothallium, the rest remaining as a reserve mass. The microspores, which are usually embedded in mucilage, undergo several divisions (forming antheridia), and liberate spermatozoids, which fertilize

Fig. 402.—Hydropterides.

[1] *Salvinia natans*, showing the floating and submerged leaves. [2] A portion of the same seen from the side, and showing the sporocarps at the base of the submerged leaves. [3] A section through two sporocarps of *Salvinia natans*; that to the left contains macrosporangia only, that to the right microsporangia. [4] *Pilularia globulifera*; one or two sporocarps are shown at the base of the needle-like leaves. [5] *Marsilia quadrifolia*, showing sporocarps. [3] × 4; the rest, natural size. (After Luerssen.)

the archegonia. From one of the archegonia the young sporophyte arises, and gradually develops into the adult form.

Salviniaceæ.—Include two genera, *Salvinia* and *Azolla*, both of which are floating plants. The former occurs in Southern Europe, the latter, though hardy in Europe, is a native of America, Australia, &c. *Salvinia* (figs. 402 [1] and 402 [2]) has a stem which lies horizontally on the water, and develops both floating and submerged leaves. The latter divide into numerous filaments, which hang down like tassels in the water (*cf.* fig. 402 [2]). They are the absorptive organs of the plant, and play the part of roots. True roots, however, are wanting, even from the embryo. The sporangia are borne on these submerged leaves close to the point of attachment to the horizontal stem, generally in three groups or sori, each of which is inclosed in a cup-like upgrowth arising from the submerged leaf (*cf.* fig.

402 [3]). The arrangement of the sori is not unlike those in *Trichomanes* (*cf.* fig. 400 [3]), except that the cup is closed round the sorus. In each sorus occur only macrosporangia or microsporangia; but in each group of three sori usually one is different from the other two. Each sorus with its investment constitutes a sporocarp. The other genus, *Azolla*, resembles a floating, leafy Jungermannia (*cf.* fig. 396 [1], p. 698); it is closely set with tiny leaves, and numerous true roots hang down into the water. The macrospores are provided with a floating apparatus and hooks; and the microspores which escape from their sporangia in packets have long barbed appendages, which become attached to the hooks of the macrospores. Thus the spermatozoids escape in the immediate neighbourhood of the female prothallia.

There are 9 species of Salviniaceæ.

Fossil residues occur in the tertiary formations.

Marsiliaceæ.—Containing the two genera, *Pilularia* and *Marsilia*. Both grow in marshy or inundated ground, and spread their rhizomes horizontally, attaching them by means of roots. The leaves in *Pilularia* (fig. 402 [4]) are needle-like, and each bears at the base a very short branch which develops into a sporocarp. In *Marsilia* (fig. 402 [5]) the leaves resemble those of *Oxalis*; near the base they give off a branch which may bear several bean-like sporocarps. The sporocarps in both these plants do not—as in the Salviniaceæ—consist of mere sori with an investment; but each is a leaf-segment in which a number of cavities develop (four in *Pilularia*, many in *Marsilia*), cavities which ultimately are quite cut off from the exterior, though they arise at first as pittings of the surface. In these cavities groups of sporangia arise—both macro- and microsporangia in each chamber. The sporocarp in this family is, therefore, in nature a leaf-lobe containing numbers of sporangial cavities, and of much greater complexity than in the Salviniaceæ. The sporocarps ultimately dehisce, the spores develop their prothallia, and fertilization takes place. There are 32 species of *Marsilia* and 3 of *Pilularia*. *P. Globulifera* alone is British. Fossils are found in tertiary formations.

Alliance XXIV.—Equisetales, Horsetails.

Possess jointed stems and small leaves inserted in whorls. The sporangia are produced on special leaves arranged in cones. All living examples are homosporous, but palæozoic forms include heterosporous genera.

Families: *Equisetaceæ*, *Calamariæ*.

The *Equisetaceæ* alone are represented by living plants, and include the solitary genus *Equisetum*, with about 40 species.

The habit of growth of the Equisetums is exceedingly characteristic. There is a branching underground rhizome from which erect aërial shoots are produced each year. From the nodes of the underground stems numerous fine roots arise (fig. 403 [2]). The whole of the aërial shoot is green and assimilating, and the leaves are represented by funnel-shaped sheaths bearing teeth inserted at the nodes. The internodes are ribbed and the whole structure harsh to the touch, and often brittle owing

to the large amount of silica contained in the epidermal membranes. The early spring shoots of many species are unbranched and terminate in spore-bearing cones (e.g. *E. arvense*, fig. 403[2]), whilst later on other branching shoots arise which are sterile (fig. 403[1]). In other cases the fertile shoots are also branched (fig. 403[7]).

Fig. 403.—Equisetaceæ.

[1] Summer sterile shoot of *Equisetum arvense*. [2] Vernal, spore-bearing shoot of *Equisetum arvense*. [3] Fertile cone of the same. [4] A single sporangiferous scale (sporangiophore) of the same. [5] and [6] Spores with "elaters" expanded and coiled. [7] *Equisetum sylvaticum* with cone. [8] Prothallium of a Horse-tail with antheridia. [1], [2], [7] natural size; [3] × 3; [4] × 6; [5], [6] × 25; [8] × 30.

The branches arise from the main axis in whorls at the base of the leaf-sheaths, and in most cases perforate the latter as they develop (fig. 403[7]). They repeat the structure of the main axis, save that they are smaller and have fewer teeth to their leaf-sheaths. *E. maximum*, common in this country in damp places, attains a height of two metres, and is the largest British representative of the group, but

E. giganteum (Tropical America) is stated to reach as much as ten metres. The Dutch Rush (*E. hiemale*) is largely used for polishing owing to the quantities of silica it contains. Characteristic of the stems of Equisetums is the large central air-space, which is only interrupted by diaphragms at the joints. Other spaces also occur associated with the vascular bundles and in the cortex, alternating with the bundles.

The spore-bearing cones (figs. 403 [2, 3, 7]) consist of stalked, shield-like leaves borne on the club-shaped termination of the axis. The scales bear numerous sporangia on their under surface (fig. 403 [4]), and in these are the curious and characteristic spores. The wall of the spore is three-layered, and the outmost layer splits away from the one below it, forming four arms attached to the spore at one point (fig. 403 [5]). These arms, termed elaters (not to be confused with the elaters of Liverworts, *cf.* p. 696) are extremely hygroscopic, and though at first coiled around the spores (fig. 403 [6]) become extended as the spores dry, and as their humidity fluctuates contract and expand again. In this way the spores become entangled with one another and are distributed in groups, arm-in-arm. The importance of this circumstance appears to be as follows:—The spores, though all of one sort (*i.e.* homosporous), give rise to dicœcious prothallia as a rule (*cf.* fig. 403 [8], representing a male prothallium); consequently it is of advantage for promoting fertilization that a number of prothallia should arise in the same neighbourhood. This result is achieved by a linking of the spores. The prothallia are richly lobed, but not unlike those of Ferns.

The *Calamariæ* are found as common fossil remains in the carboniferous formations. They include casts of the medullary cavity, impressions of the surface, and actual portions of the stems and cones in a petrified state. Many members of this family attained gigantic proportions, and their stems underwent a well-marked secondary increase in thickness. An examination of the cones shows that these former Equisetales possessed both micro- and macrospores.

Alliance XXV.—**Lycopodiales**, Club-mosses.

Forms usually with elongated, branching stems and small leaves distributed over them. The sporangia are borne on the upper surface of the leaf or in the leaf-axil; the fertile leaves are in many cases aggregated into cones. Both homosporous and heterosporous families occur.

Families: *Lycopodiaceæ, Psilotaceæ, Selaginellaceæ, Lepidodendraceæ, Sigillariaceæ, Isoëtaceæ.*

Whilst in the Filices and Equisetales several or many sporangia are present on the fertile leaves, in this alliance there is only one, and this is situated on the *upper* surface or in the leaf-axil. The sporangia in this group differ from those in many of the Filices (*e.g.* Polypodiaceæ) in being more massive and in having origin not from single epidermal cells, but from a row or group. Their form also is in many cases peculiar. The Lycopodiaceæ and Psilotaceæ are homosporous, the other families heterosporous. In the former the prothallia generally resemble those of Ferns, in

the latter their condition parallels that of the Hydropterides. Lepidodendraceæ and Sigillariaceæ are represented by fossil forms only.

Lycopodiaceæ.—The Club-mosses proper include some 100 species, distributed over various parts of the globe. The habit of a typical *Lycopodium* is indicated in the accompanying figure of *L. annotinum*, with its branching stem closely set with simple, scale-like leaves and terminal cones. The species common in mountain regions in this country are *L. clavatum*, *L. alpinum*, and *L. Selago*; *L. annotinum*

Fig. 404.—*Lycopodium annotinum.*

(fig. 404) is also met with. Of these *L. Selago* alone is devoid of cones, its sporangia occurring on the ordinary leaves. The sporangium is generally large and kidney-shaped, and is attached to the base of the upper side of the leaf (fig. 405 [4]); its concavity is directed towards the axil of the leaf. Till recently the life-history of *Lycopodium* was unknown, as difficulty was experienced in causing the spores to germinate. It was first observed in certain tropical species, *L. cernuum* and others. In this species the prothallium has the form of a tiny tuberous body, with a lobed fringe on which the antheridia and archegonia are developed. The history of development of the sporophyte from the egg has been followed and is of some interest. In *L. cernuum* the young plant consists of a tubercle bearing a tuft of

leaves above. Gradually the stem elongates and the adult form is assumed. The special interest attaching to this stage is that it is characteristic of the mature *Phylloglossum* referred to below. It has been suggested that the last-named genus is a primitive form which retains as adult character what is but embryonic in *Lycopodium*. Its prothallium resembles that of *L. cernuum*.

The genus *Phylloglossum* (found in parts of Australia and New Zealand) possesses, in addition to its tubercle and tuft of leaves, a stalk which terminates in a cone of sporangium-bearing leaves. There is only a single species.

Psilotaceæ.—Includes two genera, *Psilotum* and *Tmesipteris*. *Psilotum* is tropical; it has delicate, angular, forking stems, and its leaves are reduced to tiny scales. It is rootless and grows epiphytically. Its sporangia are three-chambered and are borne on reduced leaves. Vegetative bulbils are frequently met with, especially on those shoots which grow upon the substratum. *Tmesipteris* is also an epiphyte (New Zealand and Australia). It has conspicuous, pointed leaves and long, trailing stems. The ordinary leaves are simple, but the fertile ones fork like a V, and the sporangium (which is two-chambered) is inserted on the upper surface at the junction of the V. The prothallial stage resembling *L. cernuum* has been recently found.

Selaginellaceæ.—A family of some 300 to 400 species, which are in large part tropical, and all belong to the genus *Selaginella*. The shoots are forked and are dorsiventrally flattened. The leaves are borne in four rows—two rows of smaller overlapping leaves right and left of the median dorsal line, and two rather larger ones along the edges of the stem (*cf.* fig. 111[1], vol. i. p. 421). A very common species in the alpine regions of Europe is *Selaginella helvetica*, whilst *S. selaginoides* (= *S. spinosa*) is British. The last-named species, unlike the majority of Selaginellas, is not flattened, and its leaves are distributed around the stem as in a *Lycopodium*. A characteristic feature is the presence of a little tongue inserted in the median line of the upper surface of the leaf near its point of insertion; this is known as the *ligule*. The roots in most cases arise, not directly from the stem, but from special branches termed *rhizophores*. Selaginella is *heterosporous*. The sporangia are spherical and arise in the axils of the fertile leaves, which are collected into cones. The macrosporangia contain four macrospores, and the microsporangia numerous microspores. Both kinds of sporangia occur usually in one cone, the former below; or they may be in rows along the sides of the cones; or, finally, the two sorts of sporangia may be on different cones.

The product of germination of a microspore consists of a single, simple antheridium, containing spermatozoids, which are provided with two flagella attached to the pointed end. The macrospore produces a small, green female prothallium at one end (as in the Hydropterideæ, p. 710), whilst the rest of the spore, which here divides into large cells, serves as a reserve of food-material. The green portion bears the archegonia, and is exposed. After fertilization, an embryo arises, and gradually develops into the *Selaginella*-plant. The embryogeny presents various features of interest. In particular may be mentioned the production of a suspensor from that portion of the embryo which is towards the neck of the archegonium.

By the elongation of this suspensor the embryo proper is brought down into the aforementioned food-reserve, where it continues its development. This process is quite similar to the corresponding stage in Flowering Plants, where the suspensor is almost universally found.

Lepidodendraceæ.—This family, represented only by fossils from the Devonian and Carboniferous formations, consisted of large-growing Lycopod-like forms, with huge stems clad with linear leaves. They exhibit a secondary growth in thickness (wanting in recent Lycopods), and both micro- and macrospores were produced in the cones. Casts of *Lepidodendron*-stems bear characteristic rhomboidal areas corresponding to the leaf bases, and upon these the actual leaf-scars may be seen.

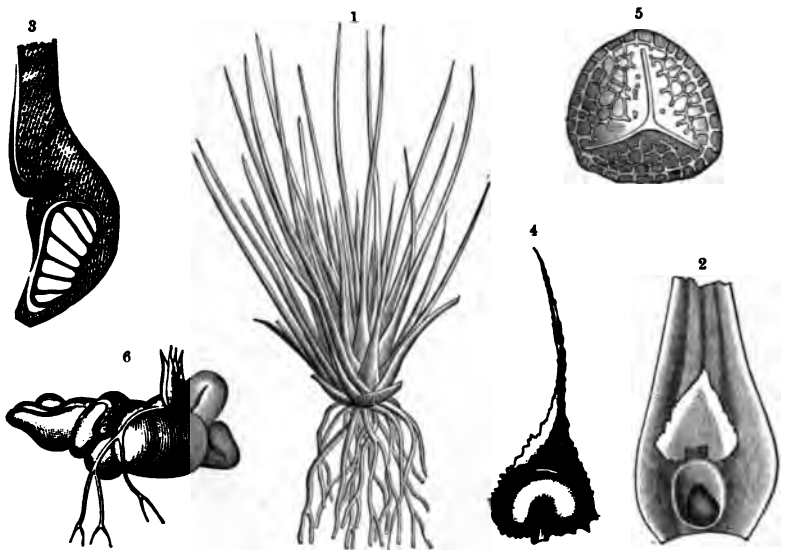


Fig. 405.—Lycopodiales.

[1] *Isoëtes lacustris.* [2] Expanded base of leaf showing the sporangium immersed in its socket and partly hidden by the velum and the ligule above. [3] Longitudinal section of base of leaf showing the strands crossing the sporangium and the insertion of the ligule. [4] Leaf from the cone of *Lycopodium clavatum* showing the kidney-shaped sporangium. [5] A single spore of *L. clavatum.* [6] Prothallium of *L. annotinum* with young plant attached. [1] natural size; [2], [3], [4], [6] × 10; [5] × 100. (After Luerssen.)

Sigillariaceæ.—Another family which flourished in carboniferous times. Like the Lepidodendraceæ, their stems are gigantic, thickened and scarred; they were also heterosporous. The marks on the stems are not rhomboidal, but shield-like, and they stand in vertical rows. The curious branching remains named *Stigmaria* constitute the root (or rhizome) of *Sigillaria.*

Isoëtaceæ.—Is a small family of aquatic mode of life, containing the single genus *Isoëtes,* which is represented by some 50 species in various portions of the globe. Unlike the other members of the alliance Lycopodiales, *Isoëtes* possesses an abbreviated stem, bearing a tuft of lance-like leaves. The common British species *Isoëtes lacustris* may serve as type of the genus (fig. 405 [1]). It grows in quantity in the mud at the bottom of upland tarns and lakes in the northern parts of the country, and is attached by delicate roots which repeatedly fork. The very short

stem is furrowed on two sides, and from these furrows arise the roots. On rare occasions it is branched. From this stem arise numerous pointed leaves, which are slightly expanded below. Each leaf bears a sporangium, immersed in a socket on its upper surface (fig. 405 [2]), and partly covering the sporangium a membrane, the velum. Immediately above the sporangium is the ligule, a little tongue-like emergence of unknown function (figs. 405 [2] and 405 [3]). Macrosporangia, containing several large macrospores, are generally found on the outer leaves, and microsporangia, with very numerous microspores, on the inner ones. The sporangia are crossed by strands of cells (*cf.* fig. 405 [3]), termed trabeculæ, but these do not partition them into chambers. The germination of the spores presents certain resemblances to the same event in *Selaginella*, but it cannot be followed out in detail here.

An interesting feature in the structure of *Isoëtes* is the existence of a cambium-like zone in the stem just outside the central bundle-cylinder. This adds new tissue, both towards the inside and outside, but most abundantly towards the outside. This latter secondary cortex is parenchymatous, but in time it becomes corky. To its formation is due the curious form of the stem.

Though many species of *Isoëtes* live below water, others are terrestrial or semi-aquatic in habit. *I. lacustris*, as it grows at the bottom of a mountain tarn, is very similar in general appearance to two flowering-plants which affect the same situation, viz., *Lobelia Dortmanni* and *Littorella lacustris*; a closer inspection, however, will readily distinguish it.

Phylum IV.—PHANEROGAMIA, Flowering Plants

The general characters of Flowering Plants have been so fully dealt with in previous sections of this work that little more is needful here beyond a bare outline of the classification of their divisions and alliances.

The Phanerogamia are characterized by the production of seeds. The macrosporangia of heterosporous Archegoniatæ are here represented by ovules, the macrospores by embryo-sacs, and the microspores by pollen-grains. The macrospore (embryo-sac) remains inside its sporangium (ovule), and here produces the reduced female prothallium (endosperm), which never has an independent existence. An egg-cell is formed within the embryo-sac, and this is fertilized by the pollen-tube which has arisen from a pollen-grain lodged upon a suitable receptive surface in the vicinity of the ovule. Ultimately, after the embryo has attained a certain differentiation, the whole macrosporangium, with contained embryo and food-material, comes away, and is known as the seed.

The oophyte or prothallial generation is thus suppressed as an independent stage in the life-cycle. The sporophyte, on the other hand, attains to a markedly more complex development than in the groups already treated. Fertilization of archegonia on free-growing prothallia by swimming spermatozoids is here replaced by a direct penetration of pollen-tubes to the ovules. To the "flower" also new duties are

allotted. In the Pteridophytes, fertile "cones" are frequently met with. They are assemblages of leaves bearing sporangia, and with the shedding of the spores accomplish their function. But in the Phanerogams it is not so. The stamens, having shed their pollen-grains (microspores), truly are done with. But the carpels which bear the ovules persist *in situ* until the ripening of the seed. And in the vast majority of Phanerogams, structures accessory to the stamens and carpels have become associated with the flower. These, forming the perianth, promote the transfer of pollen by attracting insects to the flowers in the innumerable ways already fully indicated in this volume. A minority of species depend on wind, and are destitute of attractive perianths. It is worthy of passing notice that wind-pollinated plants, though relatively few in species, are well represented in number of individuals in the various Floras of the globe. It is sufficient to instance the Conifers, Grasses and Sedges, Palms, Amentaceæ, and Urticaceæ.

The phylum Phanerogamia is divided into two sub-phyla, Gymnospermæ and Angiospermæ, which differ technically in that in the former the ovules are exposed on scales and receive the pollen-grains direct into the micropyle, whilst in the latter the ovules are borne in closed chambers, the ovaries, and the pollen is received on a special organ, the stigma

Sub-phylum A.—GYMNOSPERMÆ.

The pollen is received direct upon the nucellus of the ovule, whence the pollen-tube penetrates to the egg-cell. The embryo-sac (macrospore) is filled with the endosperm (prothallium) which bears archegonia sunk in its substance at that end which is directed towards the micropyle. In almost all cases the archegonia possess neck- and canal-cells in addition to the egg.

The phenomena accompanying fertilization and seed-production in the Gymnospermæ having been described at pp. 418 and 437, brief statements of the general external characters alone are given below.

The Gymnospermæ are divided into 3 Classes: Cycadales, Coniferæ, Gnetales.

Class I.—CYCADALES, Cycads.

Alliance XXVI.

Family: *Cycadaceæ.*

In habit the Cycads generally resemble the Tree-Ferns and Palms. They possess for the most part unbranched columnar stems terminating in a crown of large pinnate leaves. The surface of the stem is scarred with the bases of the fallen leaves, and recalls in appearance that of the fossil Lepidodendrons (*cf.* p. 716). In height Cycads do not exceed about 12 metres, and usually they do not attain even these dimensions. The flowers take the form of cones of closely aggregated scales, which vary in number from 30 to 600. The cones are respectively male and female, and

Fig. 406.—A group of *Cycas revoluta*. (From a photograph.)

are produced in close proximity to the apex of the plant, and sometimes (as in the female cone of *Cycas*) are actually terminal in position. The scales (stamens) of the male cones are usually boat- or shield-shaped, and bear very numerous pollen-sacs on their under surfaces, often aggregated into little groups or sori. The female cones are generally more massive than the male, and their scales (carpels) are shield-like or scale-like in form. In *Cycas revoluta* (*cf.* fig. 208 [7], p. 74) the carpels more nearly resemble the foliage-leaves, and the ovules are borne in the position of leaflets. In other genera the number of ovules is restricted to two. Pollination is accomplished by the wind, and the ovule as it ripens develops a hard shell enveloped in a fleshy coat. It is worthy of note that *Cycas*, *Zamia*, *Stangeria*, and probably other Cycads are fertilized by means of spermatozoids.

Cycads are restricted to the warmer regions of the globe, and are especially characteristic of the Floras of Australia (*Macrozamia*, *Bowenia*, *Cycas*) and Central America (*Zamia*, *Ceratozamia*, *Dioon*). There are nearly 80 species, belonging to 9 genera, and they have mostly a somewhat restricted distribution. Fossil remains, from the Cretaceous onwards, are abundant, and show that in former times the Cycads formed a much more important constituent of the vegetation than at the present day.

A living collection of these interesting plants is cultivated in the Palm-house in Kew Gardens; it is exceedingly rich in forms, all the genera, and a large number of the species being represented.

Class II.—CONIFERÆ.

Alliance XXVII.

Families: *Araucariaceæ*, *Abietineæ*, *Taxodieæ*, *Cupressineæ*, *Taxaceæ*.

The Coniferæ, which include the various Pines, Firs, Junipers, Cypresses, and Yews, have characteristically branched stems. The leaves are usually linear and needle-like or scaly, rarely possessing an expanded lamina. The flowers are unisexual, and occasionally the sexes are on different individuals. In by far the larger number of Conifers the flowers are cone-like, *i.e.* aggregates of scales set upon a central axis and bearing respectively ovules and pollen-sacs. The stems of Conifers thicken up in the manner characteristic of Dicotyledons, but the secondary wood is composed entirely of tracheides (fibre-shaped elements), with peculiar bordered pits (*cf.* vol. i. figs. 10 [1, 2, 4], p. 45); vessels are absent from it. In a great number of forms resin-ducts are present.

The families above given fall into two groups. The first of these includes the Araucariaceæ, Abietineæ, Taxodieæ, and Cupressineæ, and is characterized by the female flowers being cone-like. In the Taxaceæ, on the other hand, the female flowers are rarely in cones.

Araucariaceæ.—This group is familiar to everyone in the widely cultivated Chili Pine or "Monkey-puzzle" (*Araucaria imbricata*). The cones are made up of scales spirally arranged, and the ovules are solitary on the scales of the female

cones. The only other genus is *Agathis* (*Dammara*). These two genera include 14 species, distributed in the Southern Hemisphere only.

Abietineæ.—This family includes the majority of familiar Conifers of the Northern Hemisphere. They are distinguished by the fact that the scales of the female cones are divided into an upper ovule-bearing scale (the *ovuliferous scale*) and a lower subtending *bract scale*. The ovules are borne in pairs on the former,

Fig. 407.—Female Cone and Scales in Abietineæ.

[1] Cone of the Silver Fir (*Abies pectinata*). [2] Bract scale and ovuliferous scale of the same seen from the outside (the bract scale is pointed). [3] Ovuliferous scale of same seen from above, showing the two winged seeds, and the bract scale behind. [4] Longitudinal section of bract and ovuliferous scales, showing a seed *in situ* upon the latter. [5] A winged seed of the same. [6] Longitudinal section of the seed. [7] Ovuliferous scale of the Scotch Pine (*Pinus sylvestris*) seen from above; it bears two ovules. [8] Single ovuliferous scale of Larch (*Larix europæa*) showing two ovules on its surface and bract scale (with bristle) below it. [9] Longitudinal section of the ovuliferous scale of the Larch. [1] nat. size; the other figs. enlarged.

and on ripening into seeds are provided with membraneous wings in most cases. The relations of the parts of the scales and of the ovules are fully illustrated in the accompanying fig. 407. The pollen-grains also are characteristic, being in nearly all cases provided with two sac-like appendages which promote transit by wind (*cf.* fig. 217 [8], p. 98).

Included here are the Pine (*Pinus*), Cedar (*Cedrus*), Larch (*Larix*), and the

various kinds of Firs (*Abies* and *Picea*). All have needle leaves, but variously arranged. In *Pinus* the needles are borne in tufts of two (figs. 408[4] and 408[5]) or three or five. The tufts are really short branches which arise in the axils of relatively

Fig. 408.—Mountain Pine (*Pinus Pumilio*).

[1] A single polliniferous scale (stamen) seen from above. [2] Three polliniferous scales, one above the other, seen from the side. The pollen falling from each anther alights on the upper surface of the stamen next below. [3] Two spikes of polliniferous scales. [4] Branch with apical group of staminal flowers from which pollen is being discharged. [5] Female flower. 1, 2 × 10; 3 × 8; 5 × 2; 4 natural size.

inconspicuous scales (*cf.* fig. 408[5]) and though these branches are produced plentifully, permanent long branches arise only at the yearly limits of growth. The

Fig. 409.—The Scotch Pine (*Pinus sylvestris*).

Fig. 410.—The Arolla Pine (*Pinus Cembra*).

Pines may conveniently be divided into 2- and 3-leaved forms on the one hand, and 5-leaved on the other. The former agree in possessing cones of the type shown in fig. 337 [2], p. 443, in which the ends of the ovuliferous scales visible at the surface of the cone are pyramidal, whilst the 5-leaved forms are without these terminal pyramids. Among the 2-leaved Pines (20 species) are included the Scotch Pine (*P. sylvestris*, fig. 409), the Stone Pine (*P. Pinea*), the Mountain Pine (*P. humilis* or *montana*, fig. 135, vol. i. p. 549), the Corsican and Aleppo or Shore Pines (*P. Laricio* and *P. halepensis*), and many others. Of the 16 species of 3-leaved Pines the majority are North American and Oriental. The Himalayan *P. longifolia* has needles nearly half a metre long, and the Californian *P. Coulteri* cones attaining a like length.

The 5-leaved forms include about 35 species, of which the beautiful Arolla Pine (*P. Cembra*, fig. 410) is a European, and the Weymouth Pine (*P. Strobus*) a North American example.

The genus *Cedrus* is represented by 3 forms, the Cedar of Lebanon (*C. Libani*), common in Asia Minor, the Deodar (*C. Deodara*) of the Himalayas, and the Atlas Cedar (*C. atlantica*). Some authorities regard these as but varieties of one species.

The Larch (*Larix*, *cf.* fig. 337 [1], p. 443, and fig. 354, p. 483) bears its needles, which are deciduous, in tufts. The Firs which comprise the genera *Abies*, *Picea*, and *Tsuga*, differ from the Pines, &c., in that the leaves are borne directly upon the elongating branches. *Abies*, typified by the Silver Fir (*Abies pectinata*, *cf.* fig. 177, vol. i. p. 717), has erect cones (*cf.* fig. 407 [1], p. 721), with conspicuous bract and ovuliferous scales; on ripening, the scales disarticulate from the axis of the cone. *Picea*, typified by the Spruce Fir (*Abies excelsa*, *cf.* fig. 105, vol. i. p. 415), has pendulous cones, with persistent scales, and, as a rule, the bract scale remains relatively short. *Tsuga Douglasii*, the Douglas Fir, and the Hemlock Firs are in certain respects intermediate between the Silver and Spruce Firs.

In all there are 120 species of Abietineæ distributed over the cooler parts of the Northern Hemisphere.

Taxodieæ.—Are characterized by bearing more than two ovules on the scales of their cones. They include the two big *Sequoia*-species of North America, *S. gigantea*, the Wellingtonia or Californian Mammoth Tree, and *S. sempervirens*, the Red-wood, both of which attain to huge dimensions. *Taxodium distichum*, the so-called Deciduous Cypress, interesting on account of the curious knee-like roots which it produces above ground, *Cryptomeria japonica*, and *Sciadopithys verticillata*, the Umbrella Pine of Japan, all cultivated in this country as ornamental trees, are members of this group, which comprehends some 12 species in all.

Cupressineæ.—Are characterized by the fact that their cones have their scales in whorls, not spirals (*cf.* figs. 336 [6] and 336 [7] on p. 442, and figs. 337 [3, 4, 5], p. 443). They include about 80 species, amongst them the Cypress (*Cupressus*), Arbor Vitæ (*Thuja*), *Juniperus*, and other ornamental genera.

Taxaceæ.—Have generally few scales in their female cones, and sometimes, as in Taxus, the Yew (*cf.* fig. 234, p. 145, and figs. 336 [1, 2, 3, 4, 5], p. 442), the ovule is

terminal on a little shoot of its own. The seeds in this group are frequently embedded in a fleshy investment (often arillar in nature). Besides the Yews, there are included several peculiar Australasian forms, and the Maidenhair Tree, *Ginkgo biloba* (*cf.* fig. 337 [7], p. 443). There are about 70 species of Taxaceæ.

Class III.—GNETALES.

Alliance XXVIII.

Family: *Gnetaceæ.*

This family which includes three very dissimilar genera, *Ephedra*, *Gnetum*, and *Welwitschia*, is by no means easy to define. In habit they are all of them quite unlike the members of the two preceding classes, but yet they fall under the sub-phylum Gymnospermæ in view of the fact that the pollen-grain has direct access to the nucellus of the ovule and from the resemblance (rather remote) which their ovules and embryogeny presents to other Gymnosperms. They agree amongst themselves in possessing flowers with perianths, vessels in their wood, and in the absence of resin-ducts from their tissues.

Ephedra is a good example of a switch-plant, having jointed assimilating shoots with little scale-like leaves at the nodes, as in *Casuarina* or *Equisetum*. The flowers which are borne in little clusters, are small and unisexual. The male flower consists of a central columnar stamen bearing 2–8 anthers and inclosed in a 2-leaved perianth. The female flower has an ovule with one integument and a little perianth. As the seed ripens the bracts around the flower become red and fleshy. There are some 20 species scattered over the warmer regions of the globe, including the Himalayas, Mediterranean, and Mexico.

Gnetum occurs as a liane or erect tree, and has expanded leaves like a Dicotyledon, in decussating pairs. The flowers occur in clustered, catkin-like spikes, on which they are arranged in whorls. The male flowers are very like those of *Ephedra*, the female have a central ovule with 2 integuments inclosed in a flask-shaped perianth. On ripening, the perianth becomes fleshy, and the outer integument of the ovule hardens to a stone. There are 15 species, distributed in the tropics.

Welwitschia mirabilis is a plant altogether unique. Discovered some thirty-five years ago by the botanical explorer Welwitsch, it has formed the subject of a classical monograph by Hooker. It occurs in the desert regions of West Tropical Africa (Angola, Damaraland, &c.). The stem is dwarf and top-shaped (*cf.* fig. 411), and may attain more than a metre in diameter. The summit of the plant never reaches far above the surface, and it bears two huge leathery leaves which sprawl on the sand on either hand. Actually 4 leaves are produced, the 2 cotyledons, which fall away whilst the plant is still quite young, and an additional pair placed at right angles to the cotyledons and persisting throughout the life of the plant. These 2 leaves grow continually at the base whilst their apical regions become

Fig. 411.—*Welwitschia mirabilis* in its natural surroundings (from a sketch by its discoverer).

tattered and broken. *Welwitschia*, once established, does not increase much in length but continually in thickness. From the edge of its disc, in the leaf-axils, arise branches which bear cones (*cf.* fig. 411). The male cones are small, and in the axils of their scales occur flowers consisting of 6 stamens united together into a sheath and surrounding a central structure which resembles an ovary, and contains a single ovule, which is, however, so far as is known, always abortive. This ovary-like structure is provided with a trumpet-like "stigma", and the occurrence of this remarkable structure in the male flowers points to the fact that the ancestors of this plant possessed hermaphrodite flowers. The fertile female flowers occur in the axils of the scales of other much larger cones, which become bright red in colour. Each flower consists of a perianth containing an ovule with 2 integuments, but although the inner of these integuments is very long, there is no stigma-like structure as in the male flower, and the pollen-grain reaches the nucellus. The developmental history of the ovule and embryo is exceedingly peculiar—as it is also in *Gnetum*—but we cannot enter into these matters here.

Sub-phylum B.—ANGIOSPERMÆ.

Ovules contained in closed ovaries. Pollen received on a specialized portion of the carpel known as the stigma, and fertilization achieved by means of pollen-tubes which penetrate hence to the ovule.

Angiosperms fall naturally into two classes, *Monocotyledones* and *Dicotyledones*.

Class I.—MONOCOTYLEDONES.

Includes Flowering Plants whose flowers typically have their parts arranged in whorls of three, embryos with one cotyledon, vascular bundles scattered through the stem and not thickened by a cambium, leaves usually parallel-veined.

The Monocotyledones may be divided into 6 alliances:—Liliifloræ, Scitamineæ, Gynandræ, Fluviales, Spadicifloræ, and Glumifloræ.

Alliance XXIX.—Liliifloræ.

Families: *Juncaceæ*, *Liliaceæ*, *Amaryllidaceæ*, *Iridaceæ*, *Dioscoreaceæ*, *Bromeliaceæ*, *Commelynaceæ*, *Pontederiaceæ*.

In this alliance the flowers are actinomorphic, and their parts arranged in whorls of three, *i.e.* two whorls constituting the perianth, two (or one) whorls of stamens, and a whorl of three carpels united together. This condition may be briefly represented by the following formula:—P 3+3, A 3+3, G (3), in which P, A, and G stand for perianth, androecium, and gynæceum respectively. The bracket inclosing the number of carpels indicates that they are united (*syncarpous*). The ovary is 3-celled, and may be either superior or inferior; the seeds contain endosperm.

The Liliifloræ are for the most part herbs with perennial underground bulbs, corms, and rhizomes. In relatively few cases is a permanent above-ground system

Fig. 412.—Liliifloræ.

[1] *Gagea lutea.* [2] *Galanthus nivalis.* [3] *Leucojum vernum.* [4] *Colchicum autumnale,* in flower and in fruit. [5] Section of capsule of *Colchicum.* [6] *Bulbocodium.* [7] *Convallaria majalis.* [8] Stigmas and stamens of an Iris.

produced. With the exception of the *Juncaceæ* the flowers are conspicuous and brightly coloured.

Juncaceæ.—Plants of grass-like habit with inconspicuous glumaceous perianth, six stamens, and superior ovary, which is 3- or 1-celled. Pollination by wind. Pollen-grains united into tetrads. Two well-known genera represented in this country are *Juncus* (with about 190 species), which includes the Rushes, and *Luzula*, the Woodrush. In all there are some 250 species of Juncaceæ.

Liliaceæ.—Herbaceous plants with bulbs, rhizomes, and corms, conspicuous

Fig. 413.—*Asphodelus ramosus* at Paestum (Southern Italy).

flowers with petaloid perianth, stamens 6, carpels 3, united, ovary 3-celled superior. Pollination by insects. Fruits are capsules or berries.

A number of tribes may be distinguished: (1) *Colchicaceæ* having usually extrorse anthers, septicidal capsules, and distinct styles. They include *Veratrum*, *Colchicum autumnale*, the Meadow Saffron (fig. 412 [4]), which sends up its flowers in autumn, its leaves and ripening capsule next spring. *Bulbocodium* (fig. 412 [6]) is frequent in cultivation. The Bog Asphodel (*Narthecium*) also belongs to this tribe. (2) *Asphodeloideæ* include forms generally with rhizomes, rarely bulbs; anthers introrse, fruits capsular. Examples are *Asphodelus*, e.g. *A. ramosus* (fig. 413), which covers considerable tracts of country in southern Europe, forming regular plantations, and was supposed to carpet the Elysian fields; *Paradisea*

Liliastrum, a beautiful alpine plant; *Hemerocallis*, the Day Lily; *Phormium tenax*, the New Zealand Flax (fig. 414), the leaves of which yield a valuable fibre; *Kniphofia*, whose dense spikes resemble a red-hot poker, cultivated in gardens; the Aloes and their allies, chiefly African, with a permanent aërial branch-system; finally, the Australian Grass-trees (of which *Xanthorrhœa hastilis* is an example), often a conspicuous feature in the landscape, and with its long spicate inflorescence sometimes attaining a height of 3 metres or more. This plant yields a valuable gum. (3) *Allioideæ*, usually bulbous, and having flowers

Fig. 414.—*Phormium tenax*, the New Zealand flax.

in umbels. They include the Onion tribe (*Allium*, *cf.* fig. 311, p. 386), of which *A. cepa* the Onion, *A. porrum* the Leek, *A. ascalonicum* the Shallot, *A. sativum* the Garlic, *A. schœnoprasum* the Chive, and *A. scorodoprasum* the Rocambole, are cultivated. *Gagea* (fig. 412[1]) also belongs to this group. (4) *Lilioideæ* have bulbs, anthers introrse, and loculicidal capsules. Styles generally united. They include numerous familiar and beautiful plants: *Lilium* (45 species), *Fritillaria* (40 species), *Erythronium* the Dog-tooth Violet, *Tulipa* (50 species), *Scilla*, *Hyacinthus*, *Ornithogalum* the Star of Bethlehem, *Muscari*, &c. (5) *Dracœnoideæ* is an interesting tribe, as it includes the Yuccas and Dracænas, which possess a permanent aërial system, which exhibits what is very exceptional amongst Monocotyledons, a secondary thickening of the stem. *Dracœna Draco*, the Dragon-tree of

the Canaries, attains huge dimensions and a great age, and is altogether peculiar among this type of vegetation. The flowers of *Yucca* (fig. 415) are represented on p. 157, and its pollination described. (5) *Convallariaceæ* have rhizomes and berries.

Fig. 415.—*Yucca gloriosa* (from a photograph).

They include *Convallaria majalis* the Lily of the Valley (fig. 412[7]), *Polygonatum*, *Aspidistra*, *Asparagus*, *Trillium*, *Ruscus* (vol. i. p. 333), and Herb Paris (*Paris quadrifolia*)—the last-named with the parts of its flowers in fours. (6) *Smilacoideæ*, which include climbers with net-veined leaves, e.g. *Smilax*.

Fig. 416.—*Æchmea paniculata* (after Baillon).

Amaryllidaceæ.—Resemble Liliaceæ, but have inferior ovaries, and in many cases a corona to the perianth. They include the Snowdrop (***Galanthus nivalis***, fig. 412[2]), Snowflake (***Leucojum vernum***, fig. 412[3]), ***Clivia***, ***Amaryllis***, ***Crinum***, ***Narcissus*** (with well-marked corona, fig. 248, p. 177); also, ***Agave*** and ***Fourcroya*** (*cf.* vol. i. p. 657).

Iridaceæ.—Resemble Amaryllidaceæ, except that they have three stamens only, with extrorse dehiscence. The stigmas are commonly very conspicuously developed. They include the Iris (figs. 412[8] and 265), ***Crocus*** (fig. 223, p. 113), ***Gladiolus***, the flowers of the last-named being slightly zygomorphic, and many others.

Bromeliaceæ.—Possess distinct calyx and corolla. Ovary superior or inferior; fruit a berry or capsule. The family is tropical American, and very many of its members are epiphytes, showing interesting adaptations to this particular mode of life. The accompanying fig. 416 of the Peruvian ***Æchmea paniculata*** gives a good idea of their mode of growth, with rosette of tough, leathery, sword-shaped leaves and dense, terminal inflorescence. Not infrequently the bracts which accompany the flowers are very brightly coloured. Two of the chief tribes of this family are *Tillandsieæ*, with capsular fruits, hairy seeds, and entire leaves; and *Bromelieæ*, with baccate fruits and toothed leaves (*cf.* fig. 416). The former includes the rather aberrant ***Tillandsia usneoides*** (*cf.* vol. i. p. 614), a widely-distributed American epiphyte which covers trees much in the same way as does the Lichen *Usnea barbata* in temperate zones. To the Bromeliese belong numerous forms, including the *Æchmea* figured here, and the Pine-apple (***Ananassa sativa***), the various portions of the fruiting-spikes of which become entirely succulent and confluent, forming the collective fruits referred to on p. 436.

The family includes about 400, and the whole alliance over 4000 species.

Alliance XXX.—*Scitamineæ.*

Families: *Musaceæ*, *Zingiberaceæ*, *Cannaceæ*, *Marantaceæ*.

This alliance includes tropical plants with rhizomes and large conspicuous leaves. In the flowers there is more or less reduction of the androecium, often combined with a production of petaloid staminodes. The ovary is inferior, and usually 3-celled, and the seeds, which are often inclosed in arils, have perisperm. The flowers are zygomorphic, or destitute of any sort of symmetry. As a whole this alliance is one of the most remarkable amongst the Monocotyledons.

Musaceæ.—The flowers of this family agree most nearly with those of typical Monocotyledons. Of the six stamens one only is absent or developed as a staminode. The flowers are zygomorphic. They include ***Musa sapientum*** (the Banana) and *M. paradisiaca* (the Plantain), widely cultivated for their fruits; ***Strelitzia***, a remarkable South African genus, and ***Ravenala Madagascariensis***, the Traveller's Tree, so named from the water which accumulates in the excavated sheaths of the leaf-stalks. This plant attains a height of 10 metres, and has a remarkable appearance (*cf.* fig. 417) owing to the fact that its huge leaves (amongst the largest in the

Fig. 417.—The Traveller's Tree (*Ravenala Madagascariensis*). After a drawing by Selleny.

vegetable kingdom) are borne in one plane. The fruits are large capsules, and the seeds are inclosed in arils with blue metallic lustre.

Zingiberaceæ.—One stamen, the posterior of the inner whorl, alone is fertile. The two others of this whorl are joined together to form a petaloid structure—the labellum. Here are included the Ginger (*Zingiber*), *Alpinia* (fig. 283 [1], p. 289), and *Hedychium*, cultivated for the beauty of its flowers; also *Globba* and *Mantisia* (the Opera Girl) with flowers altogether remarkable; *M. saltatoria* presents some resemblance to a ballet-dancer, hence the name.

Cannaceæ.—Flowers altogether asymmetrical. The fertile stamen possesses only a half-anther and several petaloid staminodes are present forming the most conspicuous portion of the flower. *Canna indica*, the Indian-shot, and other species are much cultivated, and have given rise to numerous brilliantly-coloured hybrids.

Marantaceæ.—Have asymmetrical flowers and a fertile half-stamen only. The other stamens are modified into peculiar staminodes, and the family is nearly allied to Cannaceæ. Arrowroot is obtained from the rhizomes of species of **Maranta**.

The Scitamineæ includes about 600 species.

Alliance XXXI.—Gynandræ.

Families: *Orchidaceæ*, *Burmanniaceæ*.

Flowers with petaloid perianth and inferior ovary. The stamens reduced to one, two, or three, and generally united with the gynæceum to form a column (hence the name Gynandræ). The fruits are capsules, and the seeds exceedingly small and numerous.

Orchidaceæ.—After the Compositæ, the largest family of flowering plants, numbering some eight thousand or more species. Its members are chiefly tropical epiphytes, and their mode of life has received frequent mention in vol. i. Very characteristic of the Orchid flower is the median petal, developed as a labellum (*cf.* fig. 258[1] p. 227, and fig. 268[2] p. 255). The family may be divided into two divisions according to the number of stamens present.

Division 1. *Diandræ.*—Having usually two polliniferous stamens and a large and conspicuous staminode (which corresponds to the single fertile stamen of the Monandræ). The Lady's Slipper (*Cypripedium*, *cf.* figs. 267[1] and 267[2], p. 249, and description on p. 253) is the best-known representative of this division. A little group of plants, the Apostasiaceæ, is also included here. To it belongs *Neuwiedia*, with 3 fertile stamens (*i.e.* the two found in *Cypripedium* and the one which is represented by the staminode).

Division 2. *Monandræ.*—Includes the greater portion of the family, with one stamen only united with the gynæceum into the column and producing pollen in masses (pollen-masses). The single stamen is inserted above the stigmatic surface, from which it is separated by the rostellum, and is on that side of it which is away from the labellum, the usual alighting place for insects. The structure of the monandrous Orchid flower having been fully described and figured (pp. 253–257),

repetition is not needful here. The Monandræ may be divided into four tribes, the *Ophrydeæ*, *Neottieæ*, *Vandeæ*, and *Epidendreæ*.

The *Ophrydeæ* include most of the British and European Orchids, which are not

Fig. 418.—*Angræcum eburneum* epiphytic on a tree-trunk (Madagascar).

epiphytes but terrestrial, with swollen tuberous roots, including *Orchis*, *Ophrys*, *Gymnadenia*, *Habenaria*, and the South African *Disa*.

The *Neottieæ* also include some European forms, *Cephalanthera*, *Listera ovata* (the Twayblade), &c., and a series of colourless forms of saprophytic habit, which are destitute of foliage, including *Epipogium aphyllum* (fig. 257 [10], p. 226), *Neottia*

Nidus-avis (the Bird's Nest Orchid), and *Corallorhiza* (the Coral-root). To this tribe belongs the climbing Vanilla-orchid (*Vanilla planifolia*) the capsules of which yield the spice.

To the *Vandeæ* and *Epidendreæ* belong the numerous tropical epiphytes of which many genera are widely cultivated in greenhouses, such as *Lælia, Epidendrum, Cattleya, Masdevallia, Phajus, Catasetum*, (figs. 275 [1, 2, 3, 4, 5, 6, 7], p. 269), *Stanhopea, Vanda, Phalænopsis* (fig. 258 [1], p. 227), *Odontoglossum, Dendrobium* (fig. 275 [8]), *Oncidium, Angræcum* (fig. 418), and many others besides almost equally well known.

To give any idea of the enormous varieties of floral structure met with among the Orchids would require a whole volume. In this family of all others do we find adaptations to insect visits carried out on a gigantic scale, and in not a few cases mechanisms of singular beauty and delicacy. For full details Darwin's *Fertilization of Orchids* should be consulted.

Burmanniaceæ.—A small family of some 60 species, largely represented in Borneo and New Guinea, is of interest, as it seems to connect the highly specialized Orchidaceæ with more typical Monocotyledons like Amaryllidaceæ. They have curious flowers, with three or six stamens, and several of them are saprophytic.

Alliance XXXII.—Fluviales.

Families: *Potamogetaceæ, Naiadaceæ, Aponogetaceæ, Juncaginaceæ, Alismaceæ, Butomaceæ, Hydrocharidaceæ.*

This alliance includes a large number of aquatic forms, some with narrow, some with broad leaves. The gynæceum is superior, except in the Hydrocharitaceæ. The stamens and carpels show a tendency to an increased number as compared with typical Monocotyledons. On the other hand, many forms with reduced flowers occur. Endosperm is generally absent.

Potamogetaceæ.—Include chiefly submerged forms, some of which raise their inflorescences above the water-level, and are wind-pollinated (*Potamogeton*, fig. 419), whilst the others, including the Sea-grass (*Zostera marina*), *Zannichellia*, &c., are pollinated below the water. *Potamogeton* (Pondweed) is a large genus of some 50 species, met with in fresh and brackish water; *Zostera* grows on sandy shores between tide-levels, often forming extensive belts. The embryos in this family are peculiar. They consist of a much-thickened hypocotyl with a relatively small cotyledon inserted upon it. They are termed macropodous.

There are about 74 species of Potamogetaceæ.

Aponogetaceæ.—Contains two interesting genera, *Aponogeton* and *Ouvirandra*. The plant is submerged, and raises a spicate inflorescence (often forked) above the water. The flowers are imbedded in the spike, and consist of some 6 stamens and 3 free carpels, and a small number of perianth-segments. *Aponogeton distachus* is often cultivated in this country on account of its beautiful white flower-spikes. *Ouvirandra fenestralis* is the Lattice-leaf plant of Madagascar.

There are 15 species in all.

Alismaceæ.—Possess a 6-leaved perianth, and stamens with tendency to increase by division; carpels numerous. Here are included *Alisma Plantago*, the Water Plantain, and *Sagittaria sagittifolia*, the Arrowhead.

There are about 50 species.

Butomaceæ.—Includes *Butomus umbellatus*, the Flowering Rush, interesting from the fact that it bears ovules all over the internal surface of its carpels.

Fig. 419.—Curled Pondweed (*Potamogeton crispus*).

Hydrocharidaceæ.—Is distinguished from the foregoing families in that it includes submerged forms with inferior ovaries. The flowers are frequently unisexual, and in one form (*Halophila*) are pollinated under water, as in so many of the Potamogetaceæ. To this family belong *Vallisneria* (see fig. 155, vol. i. p. 667 and fig. 227, p. 132), *Elodea*, the American Water-weed (alluded to on p. 457), *Lagarosiphon* and *Enalus* (p. 133), *Stratiotes aloides*, the Water-soldier (vol. i. p. 552) and *Hydrocharis Morsus-ranæ*, the Frog-bit, with expanded floating leaves.

Contains about 60 species.

Alliance XXXIII.—Spadicifloræ.

Families: *Palmaceæ*, *Aroideæ*.

Monocotyledons with small and usually unisexual flowers crowded on spikes or spadices. and inclosed in one or more conspicuous sheaths, the spathes. The ovaries are superior.

This alliance may be contrasted with the group Compositæ of Dicotyledons in which also the individual flowers are merged in dense crowded inflorescences which superficially resemble single flowers (cf. *Arum* and *Chrysanthemum*).

Palmaceæ.—Include plants with cylindrical, woody stems and tough fan-shaped or feather-like leaves of large dimensions having a plaited vernation. The flowers are borne in branched, fleshy spikes often inclosed in large sheathing leaves; they are hermaphrodite or unisexual and actinomorphic; the parts are arranged in threes, and are inconspicuous. The gynæceum consists of three carpels, each containing one seed. Stamens six, pollen dust-like. Fruits are berries, drupes, and nuts, and contain three, or by suppression, one seed. The endosperm is copious, and generally hard and stony. The majority of Palms possess upright, columnar caudices surmounted by a huge tuft of crowded frond-like leaves (*cf.* vol. i. p. 289). In several species the caudex attains a height of 30 metres, and in one (*Ceroxylon andicola*) 57 metres. The Climbing Palms have slender branched stems, and by the aid of the hooks on their leaves mount to the summit of trees and stretch like lianes from crown to crown (*cf.* vol. i. pp. 363, 675, and 676). The stems of these Palms reach a length of 150–200 metres, and yield the rotang cane. The opposite figure shows the interior of a forest penetrated by Climbing Palms and two natives rolling the stems into a coil. Old Palm-stems are either smooth and show the scars of the fallen leaves, or they still bear the disintegrated fragments of former foliage-leaves. Others again are armed with spiny girdles and scales. The leaves are folded in bud and undivided, and as they unfold they split along the creases, and the blade is divided pinnately or like a fan; we may distinguish between the feather-leaved and fan-leaved Palms. Often in young Palms the leaf splits at the apex into two pointed lobes only, as in *Areca disticha*, represented in foreground of fig. 420. The dimensions of Palm-leaves and the gigantic inflorescence of the Talipot Palm (*Corypha umbraculifera*) have already been alluded to (*cf.* vol. i. pp. 287 and 745). In *Oreodoxa regia* the sheathing base of the leaf attains a length of 2 metres and a half. The fruits of many species (e.g. *Chamærops excelsa*) are borne in grape-like bunches; in others they attain to great size and weight. The Double Cocoa-nut, the fruit of *Lodoicea Sechellarum*, is prominent in this respect (*cf.* p. 452).

Most Palms are eminently tropical in their distribution. A few genera are met with throughout the tropics, others (e.g. *Mauritia*, *Oreodoxa*, and *Iriartea*) are confined to the New World; others again, as *Borassus*, *Areca*, *Kentia*, *Nipa*, *Raphia*, *Caryota*, and *Calamus* to the Old. *Chamærops humilis*, alone of the

Fig. 420.—Primeval forest in Ceylon with Climbing Palms (*Calamus*) and *Areca disticha* in foreground to the right. (Drawn from nature by v. Ransonnet.)

Palms is indigenous to Europe; *Ceroxylon andicola* is found in the Andes growing at a height of 270 metres. Fossil remains are found in the formations of the Secondary and Tertiary periods. The number of living species is about 1100.

Aroideæ.—Perennial plants with tubers, rhizomes, and climbing stems which

Fig. 421.—Aroids.

[1] *Arum maculatum.* [2] Spadix of *A. maculatum*, the spathe removed. [3] Fruiting spike of same. [4] Inflorescence of *Colocasia antiquorum.* [5] Basal portion of this inflorescence with part of spathe removed. [6] Ovary of *Colocasia antiquorum.* [7] The same in longitudinal section. [8] Columnar androecium of same. [9] *Ariopsis peltata.* [2, 5, 9] nat. size; [1, 3, 4] reduced; [6, 7, 8] enlarged.

generally bear large foliage-leaves. The flowers are borne on unbranched, fleshy spadices which are inclosed in large, expanded spathes (*cf.* figs. 421 [1, 4, 5, 9]); they are unisexual or hermaphrodite. The parts are inserted in whorls of 2 or 3; the perianth-members being inconspicuous and often absent. The androecium is very various. In *Colocasia antiquorum* (fig. 421 [8]) it consists of a whorl of stamens

Fig 422.—*Raphidophora decursiva* climbing in a primeval forest of the tropical Himalayas (from a photograph)

Fig. 423.—Climbing Aroids (*Philodendron pertusum* and *P. Imbe*) with cord-like aërial roots.

united into a single abbreviated column. Endosperm is present in the seeds. The tribe *Pisteæ* includes floating plants with leaves arranged in rosettes and propagating vegetatively by means of stolons. The *Areæ*, of which the Arum (figs. 421 [1, 2, 3]) may be taken as a type, have subterranean tuberous stems, from which arise the leaves and spadices. Numerous representatives of other tribes, including *Ariopsis*, *Caladium*, *Dracontium*, and *Amorphophallus* have tubers. *Amorphophallus titanum*, the giant of this family, has a tuber 50 centimetres in diameter, and produces umbrella-like leaves on stalks 2–5 metres long and with segments in proportion. The inflorescence is a huge spadix some 2 metres high, encircled by a sheath of beautiful mottled green with purple lining and frilled edge. When this plant flowered at Kew in 1890 (for the first and as yet only time in captivity) it was one of the sensations of a London season. It is a native of Sumatra. A few species of *Montrichardia* (*M. linifera*) and *Philodendron* (*P. bipinnatifidum*) have erect cylindrical stems, whilst the Snake-root (*Calla palustris*) and Sweet Flag (*Acorus Calamus*) have creeping rhizomes. Many tropical Aroids belonging to the tribes Monsteræ and Pothoideæ climb up the stems of trees, fastening themselves by their aërial roots, and pass from crown to crown like lianes. The Himalayan *Raphidophora decursiva* (fig. 422) is an example of this type of growth. Many of these climbing Aroids send down pendent aërial roots into the humid air of the forest (fig. 423), and these not unfrequently reach the ground, take root, and become stretched taut.

The majority of Aroids are tropical, less than 10 per cent of the species being met with in temperate regions. *Acorus Calamus*, *Arum maculatum*, and *Calla palustris* reach the furthest north. The curious *Ariopsis peltata* (fig. 421 [9]) occurs in the Himalayas to a height of 1600 metres.

There are about 900 species of living Aroids.

The *Lemnaceæ* is a little family of reduced forms allied to Aroideæ. The flowers are unisexual, and consist of a stamen and a carpel respectively. They are floating, flattened forms, and include *Lemna* (the Duckweed), and *Wolffia*, which is destitute of roots.

Associated with the Spadicifloreæ are the Pandanaceæ, which include *Pandanus utilis*, the Screw Pine (*cf.* vol. i. fig. 186, p. 758); Cyclanthaceæ, climbing and palm-like; Sparganiaceæ and Typhaceæ, marsh plants, which include *Sparganium*, the Bur-reed, and *Typha*, the Bulrush.

Alliance XXXIV.—Glumifloræ.

Families: *Gramineæ* and *Cyperaceæ*.

This alliance, which includes some 6000 species, consists exclusively of Grasses and Sedges, forms with insignificant flowers destitute of coloured perianths and pollinated by wind.

Gramineæ.—Annual and perennial plants with upright, jointed haulms, and in the case of perennials, provided with creeping rhizomes. The leaves consist of an

undivided, linear, parallel-veined lamina (vol. i. fig. 150[9]), and a sheathing basal portion. At the junction of blade and sheath is inserted a little scale—the ligule. Flowers hermaphrodite and unisexual, arranged in spikelets (*cf.* fig. 231, p. 139). Perianth absent, its place being taken in many cases by 2 tiny scales, the *lodicules*, sometimes regarded as reduced perianth-leaves. Each flower is inclosed in a sheathing scale known as a *palea*, whilst outside this and subtending the flower is a bract-like structure, the *flowering glume*; this is often awned. Every flower is thus inclosed in a palea and flowering glume, whilst the whole spikelet is inclosed in a little 2-leaved involucre consisting of 2 outer glumes. The ovary bears 2 feathery stigmas, and contains a single ovule. The stamens are generally 3 in number, though variations are met with. The pollen is dust-like. Pollination has been fully described on pp. 140–142. The fruit or grain is indehiscent, and is known as a *caryopsis*. The seed contains a floury endosperm, and an embryo placed at one side (*cf.* vol. i. figs. 141[3, 4, 5], p. 599). The internodes of the haulm are in *Zea*, *Andropogon*, *Panicum*, &c., filled with pith; in the majority of Grasses they are hollowed. The Bamboos and numerous other tropical Grasses have upright perennial stems, and form an arborescent vegetation (*cf.* vol. i. p. 713). Bamboos attain a height of 25 metres and a diameter of nearly half a metre. But the majority of Grasses produce new haulms each year from their subterranean rhizomes, and these die down at the end of the season. The female flowers of the Maize (*Zea Mais*) are borne on thick spadices (cobs) inclosed in sheathing bracts. Grasses are widely distributed over the globe, the tropics being richer in species than the temperate regions, but poorer in individuals. Grasses are found extending into arctic and alpine regions to the extreme limits of phanerogamic vegetation; thus in the Alps *Poa laxa* has been found at an elevation of 3000 metres. The Bamboos are tropical and sub-tropical; in the Steppes certain Grasses are very predominant, *e.g.* the genera *Stipa* (the Feather-grass) and *Festuca*. In moist, temperate climates, Grasses form a continuous carpet, the basis of meadow land. In marshy places and by river banks reed-like Grasses occur in great quantities (e.g. *Phragmites communis*).

Gramineæ number about 3500 species.

Cyperaceæ.—Annual and perennial plants with upright, haulm-like stems, jointed below and with long upmost segment. The leaves much resemble those of Gramineæ, but the ligule is wanting. Flowers hermaphrodite and unisexual, aggregated into spikelets, inclosed in bract-like scales. Perianth absent, or represented by scales, bristles, or hairs. The ovary is 2- or 3-carpellary. Stamens in one or two whorls of 3 each; pollen dust-like, pollination by wind. The seed contains endosperm. In the Scirpeæ the leaf-blades are frequently obsolete, and assimilation is carried on by the stems. *Scirpus lacustris* reaches a height of 1, *Papyrus antiquorum* (or *Cyperus Papyrus*, fig. 424) of 3 metres and a diameter of 10 centimetres. The pith of the larger flowering stems of this plant cut into thin strips, united together by narrowly overlapping margins, and then crossed under pressure by a similar arrangement of strips at right angles, constituted the papyrus of

Fig. 434.—*Papyrus antiquorum* in the Upper Nile.

antiquity; it grows in the Upper Nile, Syria, Palestine, &c. The stem of Papyrus bears at the summit an umbel-like tuft of filamentous branches, upon which the inflorescences arise. Cyperaceæ grow for the most part on damp moors, and by the banks of streams and lakes, and in mountain regions. Many of them are social forms, noteworthy in this respect being *Carex stricta*, which forms hummocks in marshy places, standing up above the water, often thousands together. Several Sedges, e.g. *Carex sempervirens* and *C. firma*, contribute largely to the turfy carpet of alpine slopes.

The family is distributed over the whole world. *Carex*, *Eriophorum*, and *Scirpus* are found especially in cooler and northern zones; *Cyperus* and *Papyrus* in warmer regions. About 2500 species are known.

Class II.—DICOTYLEDONES.

Flowering Plants whose flowers typically have their parts arranged in whorls of four or five, embryos with two cotyledons, vascular bundles arranged in a ring and undergoing a secondary increase in thickness, leaves more complex than in Monocotyledones and usually reticulately veined.

The Dicotyledones may be divided into three Sub-classes: *Monochlamydeæ*, *Monopetalæ*, and *Polypetalæ*. The Monochlamydeæ have a simple perianth, or in some cases the perianth may be wanting. The Sub-class is an artificial one, as it includes forms whose ancestors probably possessed a double perianth and others which are primitively simple. The Monopetalæ and Polypetalæ possess both calyx and corolla; in the former the parts of the corolla are united together, in the latter free.

Sub-class I.—MONOCHLAMYDEÆ.

Alliance XXXV.—Centrospermæ.

Families: *Piperaceæ*, *Polygonaceæ*, *Cynocrambaceæ*, *Urticaceæ*, *Chenopodiaceæ*, *Nyctaginaceæ*, *Amaranthaceæ*, *Paronychiaceæ*, *Caryophyllaceæ*.

Annual or perennial herbs, shrubs, and trees. Venation of the leaf-blades palmate or pinnate. Flowers solitary or in cymes; the cymes arranged in fascicles, glomerules, or spikes. Flowers actinomorphic, hermaphrodite, pseudo-hermaphrodite, monœcious, and dicœcious. Floral-leaves in one or two whorls; all sepaloid, all petaloid, or (in a few cases) the outer whorl sepaloid and the inner whorl petaloid. Where a corolla is developed the petals are free. In the case of dicœcious flowers there is no difference between the male and the female flowers in respect of the development of floral-leaves. The ovary is superior; 1–5-carpellary, unilocular. The ovules are borne in the centre of the ovary on a stalk which rises from the bottom of the ovary, and is sometimes long, sometimes short. Stamens 1–30, arranged in one or two whorls, the outer ones inserted in front of the sepals or sepaloid perianth segments. Fruit an achene, capsule, or berry. The seed contains an abundant farinaceous or mucilaginous endosperm. Cotyledons not thickened.

The Centrospermæ are extremely rich in inorganic salts, and in the case of many of the species soda is extracted from the ash obtained by burning the plants. The Piperaceæ contain aromatic and pungent substances; the Urticaceæ secrete enzymes in their stinging-hairs (see vol. i. p. 441). The leaves are lobed in Urticaceæ and Chenopodiaceæ, in the rest they are undivided and have entire margins. In several Chenopodiaceæ the cauline leaves are squamiform, and assimilation is then effected by the green cortex of the branches, which are transformed into phylloclades. The Piperaceæ are distinguished by a peculiar distribution of the bundles in the foliage-leaves. The lateral strands do not branch off from the midrib in the usual way, but are appressed to it and can be traced to the base of the lamina. The Urticaceæ also, particularly the genus *Parietaria*, exhibit a peculiar disposition of the bundles (see vol. i. p. 629). The Chenopodiaceæ are destitute of stipules, the Paronychiaceæ have large membranous stipules which protect the foliage-leaves, the Polygonaceæ are distinguished by curious sheathing stipules. In the Caryophyllaceæ and some Paronychiaceæ the floral envelopes are differentiated into calyx and corolla; in Nyctaginaceæ, Amaranthaceæ, and most Polygonaceæ there is a petaloid perianth, whilst in Chenopodiaceæ and Urticaceæ there is a sepaloid perianth. The perianth in Nyctaginaceæ resembles a corolla most strongly when the bracts are connate and form a sepaloid envelope or involucre, as is the case, for instance, in the Marvel of Peru (*Mirabilis Jalapa*, see fig. 425). The lowest portion of the perianth in Nyctaginaceæ continues to grow after the flower has faded and forms a leathery or woody investment to the fruit (see fig. 425 [2]). In several Chenopodiaceæ and

Fig. 425.—Nyctaginaceæ, *Mirabilis Jalapa*.

[1] Flowering branch. [2] Fruit inclosed in the persistent base of the perianth. [3] Longitudinal section through the same; the true fruit is seen within. (After Baillon.)

Urticaceæ also the perianth persists as a similar investment (e.g. *Morus*). In Amaranthaceæ the pedicels are furnished with bracts which resemble the perianth-segments and, like them, envelop the fruit. In those Centrospermæ which are destitute of floral-leaves (*achlamydeous*), *e.g.* the Piperaceæ, the floral envelopes are replaced by bracts. The Caryophyllaceæ have distinct calyx and corolla, and are often placed in the sub-class Polypetalæ; they have, however, decided affinities with the Centrospermæ. The androecium is composed of one whorl in Urticaceæ and Chenopodiaceæ, and of two whorls in most of the other families. The filaments are inflexed in the bud in Urticaceæ, but spring up when the perianth opens and so eject the pollen from the anthers (see p. 306). Most of the Centrospermæ have dust-like pollen, but in Caryophyllaceæ and Nyctaginaceæ the pollen is adhesive. In Urticaceæ and in some Caryophyllaceæ the embryo is erect, in the rest it is horse-shoe shaped or spirally curved (see fig. 425 [3]). The copious farinaceous endosperm of some Polygonaceæ and Chenopodiaceæ (*Polygonum Fagopyrum*, *P. Tataricum*, *Chenopodium Quinoa*) is used for flour. The Centrospermæ are distributed in every quarter of the globe. The Piperaceæ, Urticaceæ, Polygonaceæ, Amaranthaceæ, and Nyctaginaceæ are developed in the greatest variety in the tropics. Most Centrospermæ, however, are found in the temperate zones. The Mediterranean Flora is especially rich in Caryophyllaceæ, whilst Equatorial America abounds particularly in Amaranthaceæ and Nyctaginaceæ. The Polygonaceæ grow chiefly on the banks of streams; the Chenopodiaceæ are very prevalent by the sea-shore and on salt steppes, especially in Central Asia. Several Caryophyllaceæ flourish also on the confines of perpetual snow. *Silene acaulis* (see Plate XII.) is one of the most remote outposts of the Phanerogamia and has been met with in Franz Joseph's Land at 81° north latitude, and in the Central Alps at a height of 3160 metres above the sea-level. Fossil remains of Urticaceæ and Piperaceæ have been recognized in the deposits of the Mesozoic and Tertiary periods. The number of species now living amounts to about 4200.

Alliance XXXVI.—Proteales.

Family: *Proteaceæ*.

Perennial herbs, with underground stems which project but little above the earth, or herbs and small trees with entire or variously lobed and incised stiff foliage-leaves without stipules. Flowers in capitula or spikes (see fig. 426 [1]); actinomorphic or zygomorphic, hermaphrodite, pseudo-hermaphrodite, monœcious and dicœcious. Perianth 4-partite, petaloid; the four segments are connate at the base and, in the bud, have their free ends closed together like valves (see fig. 426 [2]). Ovary superior, free, unilocular. Number of ovules one to many. Placentation parietal. Each ovule has a double integument; the micropyle is directed towards the base of the ovary. The latter is surrounded by tissues which secrete honey. The number of stamens is equal to that of the perianth segments; the short filament is adnate to the perianth-segment behind it (see fig. 426 [3]). Fruit a drupe, a nut

a capsule or a follicle (see figs. 426[4] and 426[5], and fig. 324, p. 429). The seed contains an embryo furnished with two large, thick, fleshy cotyledons, but no endosperm.

The Proteales are for the most part much-branched shrubs. The arboreal

Fig. 426.—Proteales.

[1] *Banksia ericifolia.* [2] Single flower of *Banksia littoralis* with the spoon-shaped perianth-segments still closed. [3] Longitudinal section through the same flower; the style is in the form of a barbed hook, and the stigma rests between the anthers; the filaments are adnate to the concave surfaces of the spoon-shaped perianth-segments. [4] Fruiting spike of *Banksia ericifolia.* [5] Fruit of *Xylomelum pyriforme.* [2] and [3] magnified; the rest nat. size. (After Baillon.)

species *Knightia excelsa*, a native of New Zealand, attains a height of 30 metres. The foliage-leaves are sometimes glabrous and sometimes clothed with scales, and they possess peculiar stomata (see vol. i. p. 296). The genus *Hakea* exhibits in

some of its species pinnate and bipinnate leaves, in others cylindrical and needle-shaped leaves. The flowers, which are crowded together, are sometimes surrounded by an involucre of many scales reminding one of the involucre of Compositæ. The ovary is often borne on a special stalk. The style and stigma are very various. In many species, as, for instance, in *Banksia ericoides* and *B. littoralis* (fig. 426 [5]), the style is hooked and breaks through the perianth-tube in consequence of the excessive longitudinal growth of its lower region, but the capitate extremity remains between the anthers, which are adherent to the spoon-shaped extremities of the perianth. Only when the perianth segments disunite and open back does the top of the style become free. The pollen is often deposited upon the end of the style without, however, immediately reaching the stigmatic surface, and in many species there are special hairs or brushes for collecting the pollen, whilst pockets and recesses for its temporary reception also occur. The Proteales flourish chiefly in regions where a short rainy season alternates a long rainless period. Australia and the south-west district of the Cape are richest in species; the alliance is represented by many fewer species in the tropical region of South America, in Chili, in New Caledonia, in New Zealand, in the tropical parts of Eastern Asia, in Madagascar, and in the mountains of tropical Africa. Fossil remains of Proteaceæ occur in strata of the Tertiary Period. The number of existing species is about 1000.

Alliance XXXVII.—Daphnales.

Families: *Elæagnaceæ, Thymelaceæ, Lauraceæ.*

Annual and perennial herbs, shrubs, and trees with green foliage, or leafless parasites. Stipules absent. Flowers in fascicles (see fig. 427 [1]); actinomorphic, hermaphrodite, pseudo-hermaphrodite, or dicœcious. Perianth of one or two whorls of 2, 3 or 5 leaves each, sepaloid or petaloid. Gynæceum 1–3 carpellary. Ovary unilocular. Style single, free, at the bottom of a cup-shaped receptacle from the margin of which spring the perianth-leaves (see fig. 427 [2]). Ovule solitary. Andrœcium 1–4 whorls with 2–4 stamens in each inserted on the inner margin of the cup-shaped receptacle. Fruit a one-seeded berry, drupe, or nut. The seed contains no endosperm. The embryo is furnished with large, fleshy cotyledons.

The Cassythæ, belonging to the family Lauraceæ, are parasites poorly supplied with chlorophyll, with thin twining stems and squamiform leaves. Most of the Daphnales, however, develop woody stems with leafy branches. The leaves of Elæagnaceæ are clothed with scaly covering-hairs (see vol. i. p. 322, fig. 78 [5]). The foliage-leaves of most Lauraceæ exhibit a curious distribution of the strands in the laminæ (see vol. i. p. 631, fig. 149 [4], and accompanying fig. 427 [1]). The majority of Lauraceæ contain ethereal oils and aromatic substances. Especially to be mentioned in this connection are the Bay-Laurel (*Laurus nobilis*), the Cinnamon-tree (*Cinnamomum Zeylanicum*), and the Camphor-tree (*Camphora officinarum*). In the Sea Buckthorn (*Hippophae*, see p. 109, fig. 220), the perianth is 2- and the andrœcium 4-membered; in *Elæagnus* the perianth and andrœcium are each composed of two

2-membered whorls; in *Daphne* the perianths has two 2-membered whorls, and the androecium two 4-membered whorls (see fig. 427[3]); in *Laurus* the perianth consists of two and the androecium of four 3-membered whorls; in the genus *Gnidium* there are two kinds of floral-leaves, the lower ones sepaloid the upper petaloid in colour, and these are spoken of as calyx and corolla. The same arrangement is found in several Lauraceæ. The anthers of Elæagnaceæ and Thymelaceæ dehisce by longitudinal slits, those of Lauraceæ by valves (see fig. 427[2]). In the Elæagnaceæ the cup-shaped receptacle persists as an envelope around the fruit, and becoming succulent

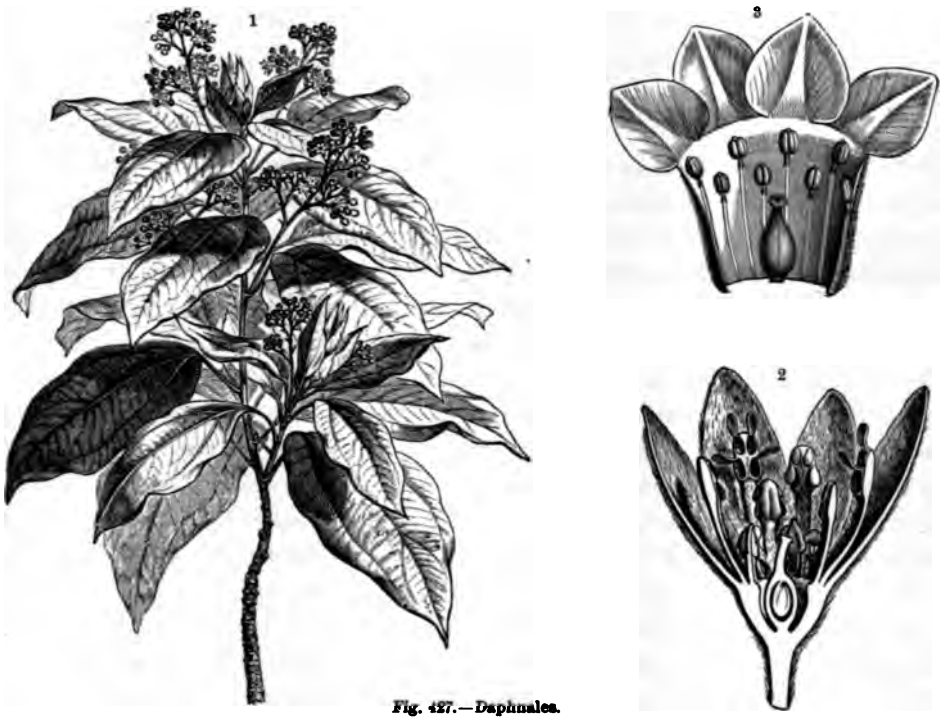


Fig. 427.—Daphnales.

[1] *Camphora officinarum* (Family Lauraceæ), flowering branch. [2] Longitudinal section through the flower of *Cinnamomum Zeylanicum* (Family Lauraceæ). [3] Flower of *Daphne Mezereum* (Family Thymelaceæ) cut open and rolled back. [1] reduced; [2] and [3] magnified. (Partly after Baillon.)

outside and strong within, the result is a false drupe. In some of the Lauraceæ also, as, for instance, in *Nectandra*, the receptacle continues to grow with the fruit, and forms a cup-shaped envelope resembling the so-called cupule in the fruit of the Oak. In Thymelaceæ and Lauraceæ the ovule is pendulous (see fig. 427[2]), in Elæagnaceæ it is erect. The Daphnales are scattered over all parts of the earth. The Thymelaceæ are best represented in countries where the climate is temperate; the Cape and Australia are particularly rich in species of that family. *Daphne striata* attains its highest elevation in the Central Alps at 2500 metres. There is a striking concentration of several species of the genus *Daphne* on a strictly limited area in the mountainous parts of Southern Europe. One of these species is the plant known in Carniola under the name of the Königsblume (*Daphne Blagayana*).

This name of King's Flower was popularly accorded to the plant because, in 1838, King Augustus of Saxony travelled to Carniola on purpose to see this rare species flowering in its restricted habitat. The Lauraceæ are principally tropical and sub-tropical plants; Eastern Asia, the Sunda Islands, and Brazil are especially rich in species of this family. The Lauraceæ reach their northernmost boundary below 50° in Eastern Asia, below 46° in Europe, and below 45° in North America. In the Southern Hemisphere the Lauraceæ range as far as 43° S. lat. Fossil remains of the Daphnales, especially of Lauraceæ, are found in the strata of the Mesozoic and Tertiary Periods. The number of existing species hitherto discovered is about 1400.

Alliance XXXVIII.—Santalales.

Families: *Santalaceæ, Viscaceæ, Loranthaceæ, Olacaceæ, Grubbiaceæ.*

Herbs, shrubs, and trees, of which most are parasitic on the roots and stems of other green-leaved Phanerogams, although they are themselves capable of assimilation owing to the presence of chlorophyll in the foliage-leaves. The leaves have entire margins; there are no stipules. Flowers actinomorphic, solitary or in cymes, which are combined into spikes, racemes, umbels, and capitula; hermaphrodite, pseudo-hermaphrodite, monœcious, and dicœcious. Perianth composed of 2- or 3-membered whorls; either sepaloid or petaloid. Gynæceum 2–3 carpellary; ovary sunk in the discoid or cup-shaped receptacle, inferior or semi-inferior, unilocular. Style single. Ovules 1–5, without integument. Stamens as many or double as many as the perianth-segments; in the former case they are inserted in front of those segments. Fruit usually a berry or drupe. Seed-coat either single or absent; the embryo either partially or entirely surrounded by fleshy endosperm.

For a description of the sinkers and haustoria of the parasitic Santalaceæ see vol i. p. 177 and pp. 205–213. Several of the Loranthaceæ have thin twining stems which put out roots, *i.e.* sinkers, from their nodes. Such of the Loranthaceæ as are destitute of green foliage-leaves have thickened and flat expanded branches. In certain Santalaceæ several bracts are united so as to form a cup-shaped involucre. In Grubbiaceæ and Olacaceæ the lower portion of the ovary is septate, at least in the first stage of development. In the Santalaceæ and some Olacaceæ 1–5 pendulous ovules are borne upon a cellular structure which is either adnate to the internal wall of the ovary or else rises freely in the cavity; in the Loranthaceæ they completely fill the ovary, and are united with the carpels into a solid mass. In Grubbiaceæ the stamens of the outer whorl alternate with the leaves of the perianth, and there are double as many stamens as perianth-segments. The stamens of the Mistletoe (*Viscum album*, see p. 87, fig. 214 [22]) are adnate to the perianth-leaves behind them, and their anthers have 6–20 loculi, each of which liberates pollen through a pore. The Santalales are widely distributed. The majority of the species are tropical and sub-tropical. The Olacaceæ only occur in the tropical parts of South America and Africa, and the Grubbiaceæ only at the Cape, whilst the Santalaceæ are chiefly natives of Africa and Australia. The

Mistletoe (*Viscum album*, found in Scandinavia as far north as 59° 30′) and several species of the genus *Thesium* reach furthest north. *Thesium alpinum* attains its highest limit in the Alps at 2400 metres. Fossil remains occur in the strata of the Tertiary Period. The number of existing species is about 750.

Alliance XXXIX.—Rafflesiales.

Families: *Rafflesiaceæ*, *Apodanthaceæ*, and *Cytinaceæ*.

Plants destitute of chlorophyll, parasitic on the roots of green-leaved woody plants. Flowering axis greatly thickened, fleshy. Flowers solitary or in racemes, hermaphrodite or pseudo-hermaphrodite. Perianth 4–6 partite. Ovary inferior. The cavity of the ovary is divided irregularly into chambers which are filled with strands and ridges bearing the ovules. Above the ovary rises a columnar style with a discoid thickening at the top, and upon the under margin of this disc the stigmatic tissue is situated. The stamens are inserted underneath the stigmatic tissue in a circle. The fruit is fleshy, baccate, and crowned by the persistent column. The seeds have hard coats. The embryo consists of few cells, has no cotyledons, and is surrounded by an oily endosperm. For a description of the suction-organs see vol. i. pp. 199–204, and for the size of the flowers see vol. ii. p. 185. The Rafflesiales live in the tropical and sub-tropical regions of both the Old and the New World; two species of the genus *Cytinus* (see vol. i. p. 201) belong to the Mediterranean flora. No fossil remains are known. The number of extant species hitherto identified is 29.

Alliance XL.—Asarales.

Families: *Aristolochiaceæ*, *Asaraceæ*.

Perennial plants, some with subterranean tuberous or creeping rhizomes, some with twining liane-like stems (see vol. i. fig. 95 [1], p. 364). Foliage-leaves broad, with entire margins, sometimes lobed. Venation apical (see vol. i. p. 633). Flowers hermaphrodite, solitary, or in cymose inflorescences, especially in axillary fascicles. Perianth of 3 petaloid leaves, united at the base. Gynæceum 4–6 carpellary; ovary inferior or semi-inferior. Styles united into a column bearing a radiating stigma. Androecium composed of 2–12 whorls of 3 stamens each. Ovules numerous in the loculi of the ovary. Fruit a capsule (see p. 431, fig. 325 [5]). The seed contains an abundant endosperm, and a very small embryo with two cotyledons.

The perianth in Asaraceæ is actinomorphic (see p. 279, fig. 279 [12, 13]), whilst in Aristolochiaceæ it is zygomorphic or else unsymmetrical, and the tube of the perianth is variously curved and inflated (see p. 166, fig. 242, and p. 226, fig. 257 [6, 7, 8, 9]). These flowers are very striking, on account not only of their form, but also of their dark-brown colour; moreover, in many cases they attain to an extraordinary size. Mention has already been made of *Aristolochia gigas* (see p. 185), and recently a Birthwort (*Aristolochia Goldeana*) has been found in West Africa which

has a perianth 66 cm. long and 28 cm. broad. In the Asaraceæ there are sometimes three small teeth alternating with the three perianth-segments, and these are looked upon as reduced inner perianth-segments. The stamens of Aristolochiaceæ are adnate to the stylar column (see p. 292, fig. 284 [12]). The Aristolochiaceæ are distributed in all parts of the world. The majority of the species are found in tropical and sub-tropical regions. The genus *Asarum* reaches furthest north. The northern limit of the Asarabacca (*Asarum Europæum*) and its highest elevation are the same as those of the Beech. Fossil remains are found in the strata of the Mesozoic and Tertiary Periods. The number of extant species hitherto identified is about 200.

Alliance XLI.—Euphorbiales.

Family: *Euphorbiaceæ.*

Annual and perennial herbs, shrubs, and trees. Flowers in racemose or umbellate cymes; actinomorphic, hermaphrodite, pseudo-hermaphrodite, monœcious, and dicecious. Floral-leaves differentiated into calyx and corolla. Calyx and corolla 3–12-merous. The corolla is often suppressed, and sometimes the calyx also is wanting. In these cases the floral-leaves are replaced by bracts and involucral leaves. The gynæceum is superior, and is composed of 3–20 carpels, which are arranged in whorls round a central column. The carpels are joined together to form a multilocular pistil. In the inner angle of each loculus are 1–2 pendulous ovules. The stamens vary in number from 1 to over 100. At the base of the flower are some peculiar glands, which are looked upon as outgrowths of the receptacle. They are either in the form of separate cellular structures, arranged in a whorl, or else are coherent in the form of a cup. In the cases where these structures do not occur they are replaced by similar glands, which are seated upon the margin of the cup-shaped involucre. The fruit is a schizocarp or drupe; sometimes it is baccate. The embryo is imbedded in an abundant fleshy endosperm.

It is difficult to describe the Euphorbiales in few words on account of their extraordinary variety. Some of them contain watery juices; the majority are full of latex. Several of the laticiferous species are poisonous. Many have green foliage-leaves; whilst some are destitute of foliage-leaves, and assimilation is then effected by means of the green cortical tissue of switch-like or cactiform branches and phylloclades. In many genera, especially in *Euphorbia*, the inflorescences have the appearance of being single flowers. A large number of male flowers are assembled together within a cup-like involucre, the free edge of which is furnished with glands as though with petals. Each of these flowers consists, however, merely of a bract and a stamen, and in the midst of them is a female flower, borne at the end of a long stalk, and resembling a stalked ovary. In many species of the genera *Croton* and *Poinsettia* the inconspicuous flowers are surrounded by bright-coloured bracts and involucral leaves. In the majority of instances three carpels are developed, which are remarkable for their rotundity. They are laterally coherent, and usually separate when mature, and become detached from the central column. The

Euphorbiales are distributed in every quarter of the globe. The majority are found in the tropics, and several arboreal species form entire woods in those regions. Some grow in marshy lowlands, whilst others inhabit steppes and the rocky declivities of mountains. *Euphorbia capitulata* grows on the mountains of the Balkan Peninsula. *Euphorbia Austriaca* stretches as far as the alpine region of the Eastern Alps. *Mercurialis perennis* attains in the Alps an elevation corresponding to the upper limit of the Beech-forests. Several annual species of *Euphorbia* are encountered as weeds in cultivated ground, as far as the limits of the arctic region. Fossil remains have not been definitely ascertained to exist. The number of extant species hitherto identified is about 4000.

Alliance XLII.—Podostemales.

Family: *Podostemaceæ*.

Perennial herbs with creeping roots which are fastened to the substratum. The shoots spring laterally from these roots, and are clothed by small scales arranged in two or three rows; these leaves are either entire or pinnately lobed, and they are sheathed at the base. Not infrequently the shoots are transformed into phylloclades, and sometimes shoots and roots are fused together into a thalloid structure. In these cases the assimilation of carbon is effected by the phylloclades as well as by the green branches of the thalloid tissue clinging to the substratum. The branches in question are ribbon-shaped or filiform, and are submerged. The flowers occur singly at the ends of the shoots, or else are sunk in the margins of the phylloclades in rows, and together form a sort of flat club. They are actinomorphic and zygomorphic, hermaphrodite, monœcious, and dicœcious. The floral-leaves are small, greenish, squamous, free, or connate, and are arranged in a 3–5-partite whorl. When the floral-leaves are suppressed, they are replaced by sheathing involucral leaves. The gynæceum is composed of 1–3 carpels; the ovary is superior, and either unilocular or else divided by delicate partition-walls into three chambers. The ovules spring from cushions of tissue which project from an axial column in the ovary. The number of stamens varies greatly, the flowers being either monandrous, diandrous, or polyandrous. In the last case the stamens are arranged in several whorls. The anthers dehisce longitudinally. The fruit is a capsule. The seeds are very small, and do not contain any endosperm. The embryo has two thick cotyledons.

The Podostemaceæ are found in running water, especially in waterfalls, clinging to rocks, loose stones, and stumps of trees which have been stripped of their bark. Almost all of them inhabit the tropics, the only exception being one species in South Africa and one in North America. No fossil remains have been found. The number of existing species hitherto described amounts to 175.

Alliance XLIII.—Viridifloræ.

Families: *Leitneriaceæ, Cannabinaceæ, Dorsteniaceæ, Artocarpaceæ, Ficaceæ, Conocephalaceæ, Moraceæ, Ulmaceæ*

Annual or perennial herbs, shrubs, and trees. The laminæ of the foliage-leaves veined with pinnate or radiating bundles. Flowers in glomerate, fasciculate, or spicate cymes; actinomorphic, hermaphrodite, pseudo-hermaphrodite, monœcious, and dicœcious. Perianth composed of 2–8 inconspicuous greenish segments. Gynæceum superior, 1–2 carpellary and unilocular. Ovule solitary, pendulous. Stamens as many or double as many as the perianth-segments; all or those of the outer whorl are

Fig. 423.—"Living bridge" formed of the aërial roots of the India-rubber and other kinds of Figs in Sikkim-Himalaya. (After Hooker.)

inserted opposite the segments of the perianth. The pollen in dusty. The fruit is a one-seeded achene or a drupe. The cotyledons of the embryo are not thickened.

The Ulmaceæ and Cannabinaceæ contain watery juices; the plants of the other families produce milky juice in greater or smaller quantity. The milky juice of the Indian *Ficus elastica* is used in the manufacture of caoutchouc, that of the South American Cow-tree (*Galactodendron utile*) as an article of diet. The milky juice of the Upas-tree (*Antiaris toxicaria*), native to Java, contains poisonous substances. In the Hop (*Humulus Lupulus*) and in the Hemp (*Cannabis sativa*) bitter and

Fig. 429.—Amentales.

[1] Birch (*Betula alba*) shoot with male and female catkins (the former at the apex). [2] Ripe female catkin of same. [3] Winged nut of same. [4] Subtending scale of fruit of same. [5] Shoot of Hornbeam (*Carpinus Betulus*) with male and female catkins (latter to right). [6] Scale of female catkin with flowers of same. [7] Scale from male catkin with stamens. [8] Scale of female catkin with ripe fruit. [3, 4, 5, 7] enlarged; the rest nat. size.

aromatic substances (lupulin and hashish) are produced in special cells and groups of cells. The curious tabular and columnar roots of the Ficaceæ have been described in detail and illustrated in vol. i. pp. 755-757. Here is represented a *Ficus* (fig. 428) with aërial roots, which Hooker saw used by the natives in the Himalaya as bridges. "The property of the fig-roots, which inosculate and form natural grafts, is taken advantage of in bridging streams, and in constructing what are called 'living bridges' of the most picturesque forms." The axis of the inflorescence is thickened in many cases, notably in the Dorsteniaceæ, Artocarpaceæ, Ficaceæ, Conocephalaceæ, and

Fig. 430.—The Oak (*Quercus sessiliflora*).

[1] Cluster of female flowers. [2] Single female flower. [3] Longitudinal section of a female flower showing the ovary with ovules, small perianth and the young cup or cupule. [4] Three male flowers. [5] Cluster of nuts (acorns) with their cupules. [6] The seed. [7] Longitudinal section of seed. [8] Transverse section of seed. [1], [2], [3], [4] enlarged; rest nat. size.

Moraceæ; sometimes it is discoid, and sometimes hollowed out into the shape of an urn (see p. 157). It also enters into the structure of certain fleshy succulent collective fruits, which afford such an important article of food in hot countries, viz. the figs of Ficus, and the Bread-fruit of *Artocarpus incisa*. Sometimes the perianth also takes part in the formation of the fruit, as, for instance, in the Mulberry (*Morus*), where it is converted into a fleshy envelope inclosing the fruit. On the other hand, in several other Viridifloræ the perianth is almost completely suppressed. In Dorsteniaceæ and Moraceæ the stamen-filaments are inflexed in the bud, and spring up after the perianth has opened, scattering the pollen-dust in the air (see fig. 229, p. 137). The filaments are straight in the flowers of the other families. The embryo is curved in most cases. There is either a very small quantity of endosperm or none at all. The Viridifloræ are found in all parts of the world. The Ulmaceæ extend

Fig. 431.—The Beech (*Fagus sylvatica*).

beyond 66° north latitude and 36° south latitude. Representatives of Viridiflorae are most abundant in the tropics. Fossil remains occur in the deposits of the Mesozoic and Tertiary Periods. The presence of leaves of a Bread-fruit tree (*Artocarpus Dicksoni*) in Greenland chalk, and of quantities of remains of Ulmaceæ (*Celtis, Zelkova, Ulmus*) in the Miocene strata, are points of special interest. The number of species ascertained to exist at the present day is about 1000.

Alliance XLIV.—Amentales.

Families: *Betulaceæ, Corylaceæ, Cupuliferæ, Juglandaceæ, Myricaceæ, Casuarineæ, Salicaceæ.*

Are all large shrubs and forest trees, forming a very conspicuous feature in the landscape in temperate climates. The flowers are unisexual and arranged in catkins or heads. Pollination is by wind, and, in the majority of cases, a perianth is wanting. In the Cupuliferæ, in which it is present, it is inconspicuous and consolidated with the ovary. The group is an exceedingly interesting one, owing to the recent discovery of several instances of chalazogamic fertilization within its limits; of this, full details were given at p. 413. In this alliance are included such familiar trees as the Birch (*Betula*, figs. 429 [1,2,3,4]), Alder (*Alnus*, p. 135), Hazel (*Corylus*, p. 147), Hornbeam (*Carpinus*, p. 433 and figs. 429 [5,6,7,8]), Oak (*Quercus*, p. 298 and fig. 430), Beech (*Fagus*, fig. 431), Chestnut (*Castanea*, p. 445), Walnut (*Juglans*), Sweet-gale (*Myrica*), *Casuarina*, and the Willow (*Salix*, pp. 299 and 424) and Poplar (*Populus*). Between 500 and 600 species have been distinguished. Members of this alliance date far back amongst the secondary rocks, and they are supposed by many to represent a primitive group of Angiosperms.

Alliance XLV.—Balanophorales.

Families: *Hydnoraceæ, Sarcophytaceæ, Cynomoriaceæ, Balanophoraceæ, Scybaliaceæ.*

Plants destitute of chlorophyll, parasitic on the roots of green-leaved woody plants, with tuberous, cylindrical, or angular stems with flowering lateral branches. The flowering axes are thickened and fleshy; the flowers hermaphrodite or pseudo-hermaphrodite, monœcious or dicœcious. Perianth of 2–8 segments, sometimes transformed into a cup on the top of the ovary, or absent and replaced by scaly bracteoles and hairs. Gynæceum 1–3 carpellary; ovary inferior, unilocular, styles either absent or 1–2 in number, filiform, and terminating in small stigmas. Stamens 1–60 inserted below the limb of the perianth. Fruit a kind of berry, nut, or drupe. The embryo is very small, has no cotyledons, and is imbedded at the top of a fleshy, oily endosperm.

For a description of the suckers and scale-leaves, see vol. i. pp. 186–198. The flowers of Hydnoraceæ are solitary; those of Balanophoraceæ, Cynomoriaceæ, and Scybaliaceæ are crowded in large numbers on unbranched clavately-thickened axes,

and those of Sarcophytaceæ on branched clavate axes. In Hydnoraceæ the cavity of the ovary is occupied by numerous ridges which project from the walls and bear the ovules; in Sarcophytaceæ, Scybaliaceæ, Cynomoriaceæ, and Balanophoraceæ the placentation is parietal, and the number of the seeds is 3 in Sarcophytaceæ, 2 in Scybaliaceæ, 1–3 in Cynomoriaceæ, and 1 in Balanophoraceæ. In Hydnoraceæ and Sarcophytaceæ there is no style, and the free upper extremities of the masses of tissue which bear the ovules act as stigmas. The Cynomoriaceæ and Balanophoraceæ have one, and the Scybaliaceæ two, filiform styles with small papillose stigmas. In Hydnoraceæ the stamens are inserted between the lobes of the perianth, and form a fleshy ring; in the other families they stand in front of the segments of the perianth; in the Balanophoraceæ the filaments are connate. Most of the Balanophoraceæ live in the tropical parts of Asia and America; a few species inhabit South Africa and New Holland. *Cynomorium coccineum*, the only species of the Cynomoriaceæ, grows in the Mediterranean area and in Western Asia (see vol. i. p. 197, fig. 42). Fossil remains are not known. The number of extant species hitherto discovered is about 45.

Sub-Class II.—MONOPETALÆ.

Alliance XLVI.—Caprifoliales.

Families: *Rubiaceæ, Caprifoliaceæ*

Annual and perennial herbs, shrubs, and trees. The foliage-leaves are opposite, stipules are present at their bases (see fig. 432[1]). The flowers are in cymes, actinomorphic and zygomorphic, hermaphrodite and pseudo-hermaphrodite. The floral-leaves are differentiated into calyx and corolla. The calyx is composed of one 2–6-sepalous whorl. The calyx-tube clothes the inferior ovary, whilst the limb consists of small green teeth. The corolla is a whorl of 3–6 connate petals (see fig. 432[3]). The gynæceum is composed of 2–5 connate carpels; ovary inferior, 2–5 locular. The placentas are axile. The andrœcium is a whorl of 3–6 stamens, adnate to the corolla-tube. The pollen is either adhesive or powdery (see p. 265). The fruit is a berry, drupe, schizocarp, or capsule. The seed contains endosperm.

Most of the Rubiaceæ are herbaceous, whilst the species of the other families are mostly shrubby and arboreal plants. In the roots of several Rubiaceæ (e.g. *Rubia tinctorum* and *Galium boreale*) there is a red colouring matter (madder-red); the Coffeaceæ and Cinchonaceæ contain alkaloids (caffeine, quinine, &c.); the sweet-scented Woodruff (*Asperula odorata*), the herb used to make the German May-wine, is famous for the kumarin it contains. No laticiferous tubes or latex, however, are contained in the tissues of any species belonging to this alliance. The foliage-leaves are always opposite and in pairs, which are at right angles to one another; the venation of the laminæ is pinnate. In the Stellatæ section of Rubiaceæ the stipules are of the same size, colour, and form as the laminæ of the opposite leaves to which they belong, and are inserted between them. The consequence is that at each node there is a whorl of leaf-structures arranged in the form

of a star. In the Cinchonaceæ and Coffeaceæ, the stipules are squamiform, and sometimes lacerated (see fig. 432[1]). In the Caprifoliaceæ they are either very small and in the form of stalked glands, or else they are adnate to the base of the petiole, and have the appearance of being narrow sessile segments of the leaf. The cymose inflorescences may be contracted into glomerules and fascicles, in which case each is surrounded by an envelope of bracts, as, for instance, in the Ipecacuanha plant (*Cephaëlis Ipecacuanha*; see fig. 432[2]), or they may form pyramidal panicles, as in the *Cinchona*, or, lastly, they may be flat cymes, as in the Elders (*Sambucus nigra*

Fig. 432.—Caprifoliales: *Cephaëlis Ipecacuanha* (Family Rubiaceæ).
[1] Entire Plant. [2] Inflorescence. [3] Single flower. [1] reduced; [2] and [3] magnified. (After Baillon.)

and *S. Ebulus*). In the Caprifoliaceæ, especially in the genera *Linnæa* and *Lonicera*, two-flowered cymes also occur, and in several species of the genus *Lonicera*, the ovaries of the two flowers in each cyme are connate. The flowers of several Caprifoliaceæ (*Linnæa*, *Lonicera*, &c.) are zygomorphic, whereas the other members have actinomorphic flowers. In the Stellatæ the fruit is a schizocarp which breaks up into two mericarps; in Cinchonaceæ, it is a capsule which dehisces from the base upwards (see p. 431, fig. 325[10]). In Coffeaceæ, Sambucaceæ, and the genus *Linnæa*, the fruit is a drupe, and in Gardenieæ and some of the Caprifoliaceæ, a berry. The baccate fruits of several species of the genus *Lonicera* (*L. alpigena*, *L. cærulea*, &c.), coalesce to form a collective fruit. Each chamber in the fruit of

Rubiaceæ, Coffeaceæ, Sambucaceæ, and of the genus *Linnæa*, contains one seed, in most Caprifoliaceæ, as in the genus *Lonicera*, several, and in the Cinchonaceæ, many seeds. The seeds of Cinchonaceæ are winged (see p. 423, fig. 318 [7]).

The Caprifoliales are distributed over all parts of the earth. The Coffeaceæ and Cinchonaceæ are chiefly tropical plants, whilst the Rubiaceæ, Sambucaceæ, and Caprifoliaceæ belong principally to the North Temperate Zone. The Cinchona is found wild only in the Cordilleras in South America (from 10° north lat. to 22° south lat.). Tropical Africa is supposed to be the original home of the Coffee-tree (*Coffea Arabica*). *Linnæa borealis*, a plant named after the Swedish botanist, Linnæus, is scattered over the Alps, in the low-lying part of Germany adjoining the Baltic, and in Scandinavia. Several species of the genus *Galium*, of the family Rubiaceæ, belong to the flora of the extreme North and of high mountains. Fossil remains have been preserved in the deposits of the Mesozoic and Tertiary Periods. The number of extant species discovered up to the present time is about 4800.

Alliance XLVII.—Asterales.

Families: *Valerianaceæ*, *Dipsaceæ*, *Calyceraceæ*, *Brunoniaceæ*, *Compositæ*.

Annual and perennial herbs, shrubs, and trees. Foliage-leaves extremely various in form but always destitute of stipules. Inflorescence a cyme or a capitulum. Flowers actinomorphic and zygomorphic, hermaphrodite, pseudo-hermaphrodite, monœcious, and dicœcious. Floral-leaves differentiated into calyx and corolla. Calyx of 2–5 sepals; the limb, which crowns the inferior ovary, is in the form of a pappus, bristles, scales, teeth, callosities, or membranous borders, and is destitute of chlorophyll. The corolla is composed of 4–5 connate petals. The gynæceum consists of 2–3 connate carpels. The ovary is inferior and contains only one developed loculus with a single ovule in it (see p. 73, fig. 207 [5]). The androecium consists of 1–5 stamens. The filiform filaments are adnate at the base to the corolla-tube. The fruit is a unilocular, one-seeded achene.

The plants belonging to this alliance exhibit for the most part herbaceous growth, but some Compositæ are shrubby (e.g. *Baccharis*), and some arboreal (e.g. *Vanillosmopsis*, *Lychnophora*). Several Valerianaceæ and Compositæ, *e.g.* the Dahlia and Jerusalem Artichoke (*Dahlia variabilis* and *Helianthus tuberosus*), are distinguished by underground tuberous structures. The inflorescence in Valerianaceæ is a much-branched cyme (see p. 305, fig. 289 [1]). In Dipsaceæ also the arrangement of the flowers is cymose, but the cymes are usually grouped together in capitula (see p. 121, fig. 225 [5]). In some genera, such as *Morina*, they are arranged in opposite fascicles in the same manner as in Labiatæ. The flowers of Compositæ are situated at the extremity of a thickened axis which is conical, hemispherical, or flat, and compressed, as the case may be; they are spirally arranged and are grouped together in capitula (see p. 242). In many cases they spring from the axils of scales ("paleæ"), or else their place of origin is surrounded by bristles. Not infrequently they spring from little depressions, and then the axis is seen to be pitted when the

flowers have fallen off. The number of flowers in a capitulum varies greatly. In many species several hundreds of flowers (florets) are crowded together, in *Adenostyles* and *Eupatorium* (see p. 320, fig. 294 [1]) there are only a few flowers in each capitulum, and in *Echinops* it is limited to a single one. The capitulum is surrounded by an involucre of bracts crowded together. The form of these involucral leaves exhibits extreme variety. In Thistles their apices are transformed into prickles, in the species of the genus *Xeranthemum*, *Helichrysum*, &c., they are like paper or parchment, dry, and distinguished by white, yellow, violet, and red colours. They preserve these characteristics unchanged even when dried, and can therefore be made up into bouquets and wreaths which do not fade. These composite flowers, which are known as "immortelles", are everywhere used as symbols of immortality and as memorial tokens. The Cape is exceptionally rich in Everlasting Flowers; among the species found there is *Helichrysum eximium*. The Edelweiss (*Gnaphalium Leontopodium*, see vol. i. p. 315, fig. 76) may also be looked upon as an immortelle, although here the bracts are not themselves dry and membranous, but are only covered with a dry, white felt of hairs. In many species the capitula are themselves grouped in capitula or glomerules. One of the most striking instances of this is afforded by the species of the genus *Haastia*, which are shown on p. 188. In the genus *Echinops* a large number of one-flowered capitula are grouped together in spherical heads, usually of a steel-blue colour. The capitula often look like single flowers, and in former times they were looked upon by botanists as compound flowers (*flores compositæ*), whence the name of Compositæ. In many species, *e.g.* the Sun-flower (*Helianthus annuus*), the capitula attain to a diameter of 40 centimetres. In the actinomorphic corollas a tube and a bell-shaped 5-partite limb may be distinguished (see p. 360, figs. 302 [1, 2, 3]). The zygomorphic flowers are either two-lipped, the upper lip being composed of one or two petals, and the under lip of four or three petals, or else ligulate, in which case the tube is greatly abbreviated and the free end of the ligule usually exhibits five segments or teeth (see p. 121, fig. 222[4], and p. 236, fig. 261 [3]). In Valerianaceæ the corolla is usually produced on one side into a kind of sac, which in the genus *Valeriana* is short and blunt (see p. 289, fig. 283 [3]), and in the genus *Centranthus* is in the form of a long, slender, pointed spur (see p. 240, fig. 263 [2], and p. 305, figs. 289 [2, 3]). In the capitula of Compositæ the flowers with tubular, ligulate, and bilabiate corollas respectively are grouped together in a great variety of ways. It is not common for all the flowers of a capitulum to have tubular flowers, but that is sometimes the case (e.g. *Eupatorium*, p. 320, fig. 294 [1]); much more frequently all the flowers in a capitulum have ligulate corollas (e.g. *Hieracium*, p. 112, fig. 222 [5]), and in the majority of instances the flowers in the middle of the capitulum are furnished with tubular corollas, and those near the periphery with ligulate or bilabiate corollas (see p. 360, fig. 302 [1]). The distribution of the sexes has been dealt with on pp. 295–297, and pp. 318–321. In the Compositæ the anthers of the five stamens are united into a tube. The anthers are not connate in the other families. In Dipsaceæ the androecium consists usually of four stamens, and in Valerianaceæ usually of three stamens (see p. 289,

fig. 283 [5]); the genera *Morina* and *Fedia* have two stamens in each flower, whilst the genus *Centranthus* (Red Valerian) has only one (see p. 240, fig. 263 [2]). For a description of the pollen of Compositæ see p. 99. The gynæceum in Valerianaceæ is composed of three carpels, and the ovary is originally 3-locular, but two of the carpels are abortive, and only the third loculus is completely developed. In the other families the ovary is unilocular from the first. The ovule and the seed resulting from its development is pendulous (see p. 178, fig. 249, and p. 240, fig. 263 [2]) in Dipsaceæ and Valerianaceæ, basal (see p. 73, fig. 207 [5]) in Compositæ. In most cases the calyx remains adnate to the mature fruit and assumes the form of a crown of hairs or bristles, which is termed a "pappus" (see p. 432), or else constitutes a membranous limb. In a later chapter we shall deal with the significance of these structures. In the Dipsaceæ the fruit is surrounded by a saccate involucre called an involucel. The alliance is distributed over all parts of the earth; its members flourish both in the tropics and in the arctic regions, and are met with on the seashore and by the side of glaciers, in bogs and on arid ground, in shady woods and on sandy steppes. The greatest number are natives of the North Temperate Zone. In the Himalayas several Composites occur at an elevation of 4500 metres. Fossil remains have been found in small quantities in the deposits of the Mesozoic and Tertiary Periods. The number of extant species identified up to the present time is about 10,700.

Alliance XLVIII.—Campanales.

Families: *Campanulaceæ, Lobeliaceæ, Stylidiaceæ, Goodeniaceæ.*

Annual and perennial herbs with entire exstipulate foliage-leaves arranged spirally. Flowers in capitula or racemes, or else solitary; actinomorphic or zygomorphic, hermaphrodite or pseudo-hermaphrodite. Floral-leaves differentiated into calyx and corolla. Calyx of one whorl of 3–8 sepals, corolla of one whorl of 3–8 petals. The calyx-tube clothes the inferior ovary, and the calyx-limb is in the form of 3–8 comparatively large, green segments which crown the top of the ovary. The petals are joined. The gynæceum is composed of 2–5 connate carpels; the ovary is inferior and 2–5 locular. The ovules are numerous, and are borne on axile placentas. The androecium consists of one whorl of 3–8 stamens, which are attached to the bases of the petals. The filaments are free; in the young flower the anthers are in close contact, forming a tube surrounding the style (see p. 360, figs. 302 [10, 11]). Sometimes they are connate, and in that case the tube persists even when the flower begins to fade. The pollen is adhesive. The fruit is a capsule (see fig. 340 [1], p. 448).

All the Campanales have laticiferous tubes running through them, and in several species the leaves and stems are copiously supplied with latex. The flowers are actinomorphic in Campanulaceæ, zygomorphic in the other families. In the Stylidiaceæ, only two of the stamens develop pollen capable of effecting fertilization, whilst three stamens are abortive; in the other families all the stamens produce

pollen, which ripens effectually. The Campanales are distributed over all quarters of the globe. The Campanulaceæ are mostly natives of the North Temperate Zone, the Lobeliaceæ of the South Temperate Zone and the Tropics. Some Campanulaceæ are also found amongst the flora of the Arctic regions, and of high mountains. The Stylidiaceæ and Goodeniaceæ are confined to Australia. No fossil remains have been discovered. The number of identified species now living is about 1300.

Alliance XLIX.—Ericales.

Families: *Diapensiaceæ, Pyrolaceæ, Monotropaceæ, Lennoaceæ, Arbutaceæ, Rhodoraceæ, Ericaceæ, Epacridaceæ, Empetraceæ, Ebenaceæ, Sapotaceæ.*

Perennial herbs, shrubs, and trees. Flowers actinomorphic and zygomorphic, hermaphrodite, pseudo-hermaphrodite, monœcious, and dicœcious. The floral-leaves arranged in two 3–5 partite whorls. The lower whorl constitutes a calyx, the upper a corolla. The petals are free in Pyrolaceæ and Monotropaceæ; in the other families they are coherent, at any rate at the base. The gynæceum is composed of 3–10 carpels; the ovary is superior, and 3–10 celled. The ovules arise from an axile placenta. The andrœcium is composed of one or more whorls of 4–5 stamens each. In many cases some of the stamens are metamorphosed into gland-like structures. The fruit is a capsule, berry or drupe. The embryo is erect, and imbedded in the fleshy endosperm.

The Diapensiaceæ and Pyrolaceæ (see figs. 277 [7, 8] p. 273), are perennial herbaceous, or suffruticose plants, which grow in black humus, and have stiff, evergreen foliage-leaves; the Monotropaceæ and Lennoaceæ are parasites or saprophytes (see vol. i. p. 252), and are destitute of chlorophyll. The Arbutaceæ, Rhodoraceæ, Ericaceæ, Epacridaceæ, and Empetraceæ are, for the most part, dwarf shrubs; only a few are trees. *Erica arborea*, one of the Mediterranean Flora, when able to grow without hindrance, attains the height of 8 metres. The branches of Ericaceæ, Epacridaceæ, Empetraceæ, and of *Loiseleuria* or *Azalea procumbens*, one of the Rhodoraceæ, are thickly covered with stiff, rolled leaves (see vol. i. p. 301 [2]). The species of the genus *Rhododendron* have flat foliage-leaves, as have also the Arbutaceæ (see fig. 433[1]). The leaves of *Arctostaphylos alpina*, *Azalea Pontica*, and *A. mollis* are green in the summer only, whilst most of the Arbutaceæ and Rhodoraceæ have flat, evergreen foliage. The Ebenaceæ and Sapotaceæ exhibit, in a large proportion of their species, arboreal growth and leathery foliage-leaves. All the Ericales are distinguished for their solid timber. Some of the Rhodoraceæ have zygomorphic flowers; the rest of the Ericales have actinomorphic flowers. In *Loiseleuria*, and in the Empetraceæ and Epacridaceæ, the androecium is composed of one whorl; in the others it consists of two or more whorls. The anthers of Arbutaceæ and of many Ericaceæ possess two peculiar horn-like appendages (see figs. 433[3] and 433[4], and figs. 216 [9, 10, 11] p. 91). In Epacridaceæ the anthers are unilocular, and dehisce longitudinally; in Ericaceæ, Arbutaceæ, Rhodoraceæ, and Pyrolaceæ they usually open by terminal chinks or pores (see p. 91, figs. 216 [8, 9, 10, 11, 12]).

The pollen is dusty in Ericaceæ, but adhesive in most other cases. The pollen-cells are united in fours in Ericaceæ, Rhodoraceæ, and Pyrolaceæ, and in the Rhodoraceæ these groups are connected by tough threads (see figs. 219 [2, 3, 4] p. 101). The fruit is capsular in Diapensiaceæ, Pyrolaceæ, Monotropaceæ, Rhodoraceæ, Ericaceæ, and Epacridaceæ, and baccate in Arbutaceæ, Empetraceæ, Sapotaceæ, and Ebenaceæ. In the Lennoaceæ the fruit resolves itself into 10–28 one-seeded portions. The Ericales are distributed over the whole world; the Ebenaceæ and Sapotaceæ live chiefly in the tropics; the Lennoaceæ are confined to the southern half of North America, and the Epacridaceæ to Australia. The species of Ericaceæ are most abundant at the Cape. Most of the species of the genus *Rhododendron* inhabit

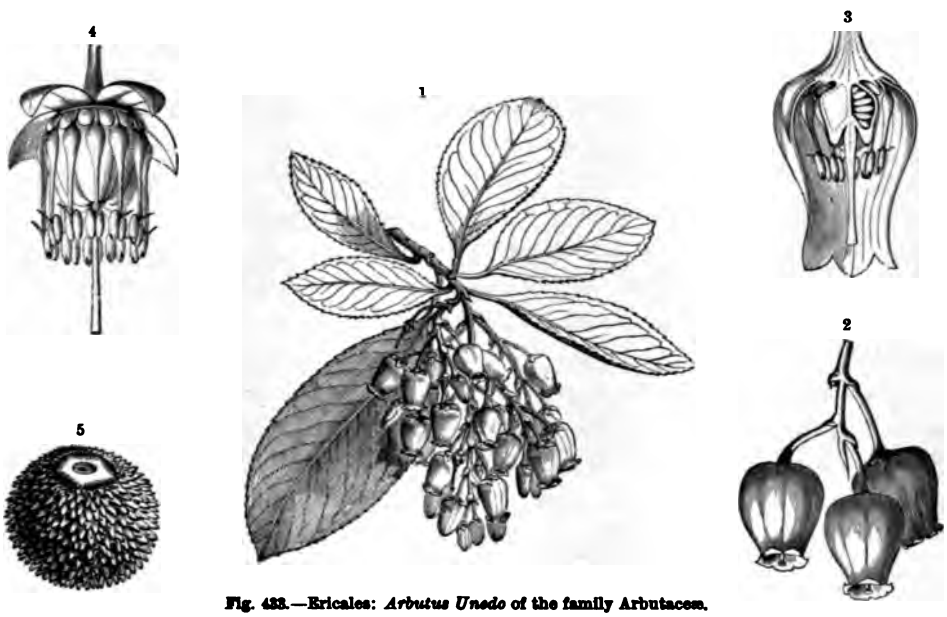


Fig. 433.—Ericales: *Arbutus Unedo* of the family Arbutaceæ.

[1] Flowering branch. [2] Three flowers magnified. [3] Longitudinal section through a flower. [4] Flower from which the corolla has been removed. [5] Papillose berry. [2], [3] and [4] magnified. (After Baillon.)

the mountains of Central Asia, *e.g.* the Himalayas. The genus *Kalmia* belongs to the mountains of North America. The Diapensiaceæ live in the arctic regions, as also do several Ericaceæ. *Loiseleuria* or *Azalea procumbens* is widely distributed in the arctic regions, and also occurs in exactly the same form on the mountains of Central and Southern Europe; in the Central Alps it attains its maximum elevation of 2700 metres above the sea-level. Most of the Ericales grow sociably on rocky declivities in mountainous districts, and on sandy soil in plains. Many only flourish on moorland, or when rooted in a deep layer of humus, and these play an important part in the formation of peat. Fossil remains are found in the deposits of the Mesozoic, Tertiary, and Diluvial periods. The number of extant species known is about 2300.

Alliance L.—Vacciniales.

Families: *Vacciniaceæ, Oxycoccaceæ.*

Woody plants, presenting all gradations in form, from that of delicate dwarf shrubs lying upon the ground to that of stately trees. The foliage-leaves arranged spirally, exstipulate. Flowers in racemes and fascicles, or solitary; actinomorphic, hermaphrodite. Floral-leaves differentiated into calyx and corolla. The calyx is composed of a whorl of 4–6 sepals. The calyx-tube clothes the inferior ovary; the calyx-limb is in the form of short, green teeth, crowning the top of the ovary. The corolla consists of a whorl of 4–6 petals; the petals are united or free. The gynæceum is composed of 4–6 connate carpels. The ovary is inferior and 4–6-locular. The placentas are axile. A honey-secreting tissue is situated on the top of the ovary. The andrœcium consists of two whorls with 4–6 stamens in each. The stamens surround the nectary, and are free from one another and from the corolla. The members of the outer whorl are opposite the petals. The fruit is a berry or a drupe. The seed contains a fleshy endosperm.

The Vacciniales have no laticiferous tubes or latex. In Vacciniaceæ the petals are united, and the anthers are furnished with horn-shaped appendages, in Oxycoccaceæ the petals are free, and the anthers have no horns. The Vacciniales are distributed in all quarters of the globe, and in all latitudes. The species which belong to the Temperate Zones grow in peat-bogs and in the humus of woods and heaths, the species native to the mountains of tropical regions are, in some cases, epiphytic on the bark of old trees. Many are of social habit, and cover extensive tracts of ground. This is the case, for instance, with the various species of the genus *Vaccinium*: the Cow-berry (*Vaccinium Vitis-Idæa*), the Bilberry (*Vaccinium Myrtillus*), and *Vaccinium uliginosum*. These species are also found within the area of the Arctic Flora. *Vaccinium uliginosum* ranges furthest to the North, and in Greenland forms with the dwarf Birch (*Betula nana*) and dwarf Willows, a low undergrowth which reaches to 73° N. Lat. They clothe the mountain sides in the Central Alps as far as 2400 metres above the sea-level. Fossil remains have been found in the deposits of the Mesozoic, Tertiary, and Diluvial Periods. The number of extant species hitherto recognized amounts to about 350.

Alliance LI.—Primulales.

Families: *Primulaceæ, Plumbaginaceæ, Myrsinaceæ.*

Annual and perennial herbs, shrubs, and small trees with alternate, opposite, and verticillate foliage-leaves. Fowers solitary, or in spikes and racemes; actinomorphic, hermaphrodite or pseudo-hermaphrodite. The floral-leaves are arranged in two whorls of 4–8 segments each. The lower whorl constitutes a calyx, the upper a corolla. The petals are coherent. The pistil is superior, 5-carpellary, unilocular. The ovules are supported in the middle of the ovary on a column of varying length

rising from the bottom of the ovary. The stamens, five in number, are inserted in front of the petals, and are adnate to them (*epipetalous*). The fruit is a unilocular capsule or drupe. The seeds contain an endosperm, in which the embryo is embedded.

The ovary is surmounted by a single style in Primulaceæ and Myrsinaceæ, by five styles in Plumbaginaceæ. The capsules of Primulaceæ are many-seeded, those of Plumbaginaceæ are one-seeded. In the genus *Glaux* only one floral envelope is developed. It has the appearance of a perianth, and resembles that of Polygonaceæ. It is interpreted as being a petaloid calyx. The fact that in *Glaux* the stamens occupy the same position in relation to the sepals as the petals do in other cases warrants our supposing that what is usually designated as the corolla in Primulaceæ is only a whorl of stamens with connate petaloid filaments. The Primulaceæ are distributed mainly in the temperate zone of the Northern Hemisphere. Most of the species of the genera *Primula*, *Soldanella*, and *Androsace* are alpine plants. The Alps and the Himalayas are particularly rich in these species. *Androsace glacialis* (see fig. 221 [6]) occurs in the Alps in the neighbourhood of glaciers at a height of 3160 metres above the sea-level. *Primula pubescens*, a plant obtained by Clusius in 1582 from the Gschnitzthal in Tyrol, was the original species from which Auriculas were derived during the fashion for their cultivation which prevailed in the seventeenth century. The Plumbaginaceæ are represented by large numbers of species on the shores of the Mediterranean and in the saline steppes of the East. The Myrsinaceæ grow exclusively in the tropics. Fossil remains of Myrsinaceæ are known amongst the deposits of the Tertiary period. The number of species now existing is about 1100.

Alliance LII.—Tubifloræ.

Families: *Gentianaceæ*, *Asclepiadaceæ*, *Apocynaceæ*, *Loganiaceæ*, *Convolvulaceæ*, *Polemoniaceæ*, *Hydrophyllaceæ*, *Boraginaceæ*, *Nolanaceæ*, *Solanaceæ*, *Scrophulariaceæ*, *Lentibulariaceæ*, *Bignoniaceæ*, *Acanthaceæ*, *Gesneraceæ*, *Orobanchaceæ*, *Globulariaceæ*, *Plantaginaceæ*, *Myoporaceæ*, *Verbenaceæ*, *Labiatæ*, *Oleaceæ*, *Jasminaceæ*.

Annual or perennial herbs, shrubs, and trees. Flowers actinomorphic and zygomorphic, hermaphrodite and pseudo-hermaphrodite. Floral-leaves in two 4–5-partite whorls; the lower whorl in the form of a calyx, the upper in the form of a corolla. Petals united. Gynæceum 2- or more celled, ovary superior. The ovules are developed either on the turned-in margins of the carpels or on an axile placenta. The androecium is composed of a whorl of 2–5 stamens. The fruit is either a succulent berry, a capsule with various modes of dehiscence, or a drupe.

The Solanaceæ, Scrophulariaceæ, Loganiaceæ, and Asclepiadaceæ contain poisonous alkaloids, the Gentianaceæ contain bitter substances, and the Labiatæ contain etherial oils and aromatic substances. The majority of Tubifloræ possess green foliage-leaves. Some Scrophulariaceæ, *e.g.* the species of the genus *Rehmannia*, are

in the form of switch-shrubs, and several Asclepiadaceæ, *e.g.* the species of the genus *Stapelia*, have cactiform stems. In these the assimilation of carbon is effected by the green cortical tissue. The Orobanchaceæ are parasites destitute of chlorophyll (see vol. i. p. 183). Amongst Convolvulaceæ, and more especially amongst Scrophulariaceæ, there are many species which live as parasites and saprophytes, and are partially deficient in chlorophyll (see vol. i. pp. 171–183). An account has already

Fig. 434.—Acanthaceæ.
Acanthus mollis on the coast of Dalmatia.

been given of the way in which the Lentibulariaceæ, *e.g.* the species belonging to the genera *Utricularia* and *Pinguicula*, derive a portion of their food from the bodies of insects which are caught by them (see vol. i. pp. 120, 140). In Gentianaceæ, Oleaceæ, Apocynaceæ, Asclepiadaceæ, Convolvulaceæ, and many Boraginaceæ and Solanaceæ the corolla is actinomorphic. The Labiatæ, Scrophulariaceæ, Verbenaceæ, Acanthaceæ, Lentibulariaceæ, and some genera of Boraginaceæ and Solanaceæ bear distinctly zygomorphic flowers. In the Ash genus (*Fraxinus*), which belongs to the family of Oleaceæ, the corolla is often entirely suppressed. Most Labiatæ have four

didynamous stamens, but some of them, *e.g.* those of the genus *Salvia* (see fig. 271, p. 262), have two stamens, as have also the species of the genus *Veronica* (see fig. 257, p. 226) of the family Scrophulariaceæ, and the majority of the Jasminaceæ and Oleaceæ (see fig. 283 [2]). Most of the Tubifloræ possess five stamens. The curious modification of the androecium of Asclepiadaceæ has been fully described on p. 257,

Fig. 435.—Ranunculaceæ.

[1] *Helleborus niger* (reduced ½). [2] *Myosurus minimus*, complete plant with flowers and flower-buds (nat. size). [3] A single flower of *Myosurus* (magnified).

et seq. In the Apocynaceæ the two opposite carpels are separate at the base and connate at the upper end only. The fruit of Labiatæ and Boraginaceæ resolves itself when it is ripe into four one-seeded nutlets. The seeds of Apocynaceæ and Asclepiadaceæ are furnished with a plume of hairs. In most of the Tubifloræ the base of the pistil is partially or completely surrounded by swollen tissue which

secretes honey. The Tubiflorae are distributed in every quarter of the globe. Several families, such as the Loganiaceæ and Bignoniaceæ, are confined to tropical and sub-tropical regions. The Acanthaceæ also chiefly inhabit the warmer parts of the earth. The genus *Acanthus* grows particularly in the region of the Mediterranean Flora. The leaves of several species of *Acanthus*, e.g. *Acanthus spinosissimus* (see vol. i. fig. 116, p. 437) and *Acanthus mollis* (see fig. 434), frequently served the Greek and Roman sculptors as patterns for their ornaments. The genus *Stapelia*, of the family Asclepiadaceæ, is confined to the Cape; the Labiatæ are most abundantly represented in the Mediterranean Flora; the Gentianaceæ and Scrophulariaceæ inhabit mountainous regions of the Old and the New World in large numbers of different forms, and several species of the genera *Gentiana, Veronica, Euphrasia*, and *Pedicularis* thrive best in proximity to glaciers both in mountain districts and in the arctic regions. Fossil remains occur in the strata of the Tertiary period. The number of species now living which have been identified up to the present time is about 16,500.

Class III.—POLYPETALÆ.

Alliance LIII.—Ranales.

Families: *Ranunculaceæ, Dilleniaceæ, Calycanthaceæ, Magnoliaceæ, Anonaceæ, Menispermaceæ, Berberidaceæ, Lardizabalaceæ, Nymphæaceæ.*

Stamens rarely definite. Carpels, free or immersed in the receptacle, very rarely connate. Embryo minute, embedded in a fleshy endosperm. In the Ranunculaceæ the petals are not infrequently modified into honey-glands, and the sepals petalline. The carpels are free from one another, and sometimes indefinite and spirally arranged, sometimes definite and whorled. In *Calycanthus*, the parts of the flowers are inserted in a continuous spiral upon a hollow receptacle, and pass gradually the one into the other. In Berberidaceæ, the anthers open by means of valves. The Nymphæaceæ include marsh and water plants (e.g. *Nymphæa, Nuphar, Nelumbium*, the Indian Lotus, figured opposite). In several of these the carpels are united together into a large ovary with shield-like stigmatic disc. In *Nelumbium* (*cf.* fig. 334, p. 440), the carpels are borne in distinct sockets. The fruit in the alliance is very varied, and includes achenes, follicles, berries. Fossil remains occur in the Tertiary Strata. Total number of living species about 3000.

Alliance LIV.—Parietales.

Families: *Sarraceniaceæ, Papaveraceæ, Fumariaceæ, Cruciferæ, Capparidaceæ, Moringaceæ, Resedaceæ, Cistineæ, Violaceæ, Bixaceæ.*

Annual and perennial herbs, shrubs, and trees. Flowers solitary or in spikes, umbels, racemes, and racemose cymes; actinomorphic and zygomorphic, hermaphrodite and pseudo-hermaphrodite. Floral-leaves differentiated into calyx and corolla; the calyx composed of a 2–5-partite whorl, the corolla of two 2-partite

whorls or one 5-partite whorl. Petals free. Gynæceum composed of 2, 3, or several carpels joined together to form a unilocular (or spuriously bilocular), free, superior ovary. Ovules attached to the interior walls of the carpels on ridges, or springing directly from the walls of the ovary (see fig. 437 [1]). The andrœcium is composed of either one whorl or many whorls of 2–5 stamens; the stamens are free, and generally of equal length, and are not joined together or to the corolla (see fig. 243, p. 168). The fruit, in most cases, is a many-seeded capsule (see fig. 437 [2]); in the genus *Fumaria* it is a small one-seeded drupe (see figs. 322 [1] and 322 [2], p. 427).

Fig. 436.—*Nelumbium speciosum*, the Indian Lotus, growing in a marsh, near Pekin (from a photograph).

In the Capparidaceæ, it is borne on a long stalk. The Resedaceæ are interesting, in that in many of them the ovary is open from the beginning, the stigmatic tissue being formed by the swollen lips. The Cruciferæ form a large and important family of over 200 genera. For systematic purposes they are divided into the following tribes:—Pleurorhizeæ, Notorhizeæ, Orthoploceæ, Spirolobeæ, and Diplocolobeæ. Annual or perennial herbs and suffrutices with the foliage-leaves in spirals, venation pinnate. Flowers in racemes, hermaphrodite, pseudo-hermaphrodite, actinomorphic and zygomorphic. Floral-leaves differentiated into calyx and corolla, each of which is composed of two 2-merous whorls. Petals free. Ovary free, superior. The carpels spring from below the end of the conical receptacle, and are of two kinds: the two lower carpels bear no ovules, but form valves, whilst the two

upper are transformed into ribs and form a framework to which the valves are applied. The two superior carpels are separated by a thin membrane, and bear the ovules in two rows (see p. 75). The androecium is composed of two short and four long stamens (see p. 292, fig. 284[8]). The pollen is adhesive. The fruit is a siliqua (see p. 75 and p. 431, fig. 325[15, 16]). The seeds have no endosperm. The embryo is curved. The cotyledons and also the foliage-leaves and roots of most Cruciferæ contain pungent and oily substances, particularly Oil of Mustard, as is well known in the cases of the Mustard-plant, Water-cress, Garden-cress, Radish, and Horse-radish.

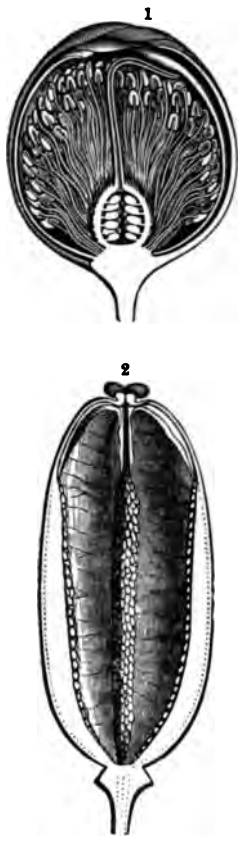


Fig. 437.—Parietales.

[1] *Bixa Orellana* (Bixaceæ). Longitudinal section through a flower-bud which is about to open. [2] *Argemone Mexicana* (Papaveraceæ). Longitudinal section through the ovary. (Magnified.)

The Cruciferæ are distributed over the Northern Hemisphere. They occur in greatest variety in the steppe-districts of the Old World. The Mediterranean, Arctic, and Alpine floras also include large numbers of these plants. Amongst those Phanerogams which survive at the very confines of vegetation in the Arctic regions, and on mountains, are to be reckoned several Cruciferæ. No fossil remains are known.

The Sarraceniaceæ are marsh- and water-plants, and their leaves are adapted to the capture of insects (see vol. i. p. 143 *et seq.*), whilst the rest of the Parietales grow chiefly on rocky or sandy ground. The Parietales are distributed over the warm and temperate parts of the Old and the New World; the Cistaceæ belong especially to the flora of the Mediterranean. The only known instance of fossil remains is the fruit of a Poppy which was found in a deposit of the Tertiary Period. The number of extant species hitherto identified is about 3000.

Alliance LV.—Malvales.

Families: *Malvaceæ, Sterculiaceæ, Tiliaceæ.*

Flowers actinomorphic, parts in whorls of 5. Sepals free or connate, often valvate in bud. Stamens various, often united. Carpels 3 to indefinite, united. Placentation axile; seeds with endosperm. The Malvaceæ often possess an epi-calyx; fruit usually splitting into 1-seeded mericarps. They include the Mallows (*Malva*), Cotton-plants (*Gossypium*), Hollyhock (*Althæa*), &c. The Tiliaceæ are represented by the Linden (*Tilia*), and the Sterculiaceæ include *Theobroma Cacao*, from which chocolate is derived.

There are nearly 200 species in this alliance.

Alliance LVI.—Discifloræ.

Families: *Linaceæ, Erythroxylaceæ, Oxalidaceæ, Humiriaceæ, Malpighiaceæ, Zygophyllaceæ, Geraniaceæ, Balsamineæ, Tropæolaceæ, Rutaceæ, Aurantiaceæ, Diosmaceæ, Zanthoxylaceæ, Simarubaceæ, Ochnaceæ, Burseraceæ, Meliaceæ, Ilicineæ, Celastrineæ, Rhamnaceæ, Ampelideæ, Sapindaceæ, Acerineæ, Hippocastaneæ, Sabiaceæ, Terebinthaceæ.*

Annual and perennial herbs, shrubs, and trees, with simple and compound foliage-leaves. Flowers actinomorphic and zygomorphic, hermaphrodite, pseudo-hermaphrodite, monœcious and dicœcious; arranged in varying types of inflorescence. Floral-leaves in two 4–5-merous whorls; the lower whorl a calyx, the upper a corolla. The gynæceum is composed of a whorl of carpels borne on a swollen disc. Ovary superior. Each carpel has a separate loculus. In Aurantiaceæ and Ampelideæ the carpels are completely united so as to form a single pistil; in Rutaceæ and Zygophyllaceæ they are united at the base and form a lobed ovary, whilst in Zanthoxylaceæ, Ochnaceæ, and Simarubaceæ, they are quite separate (see fig. 438 [6]). In Terebinthaceæ only one carpel is developed, but there are usually traces of suppressed carpels close to it. The ovules are in the inner angles of the loculi; in Aurantiaceæ, Rutaceæ, and Zygophyllaceæ their number exceeds two in each loculus, in the other families it is only 1–2. The stamens are arranged in 1–2 whorls, and number 4–5 in each whorl; they spring from the edge or from the surface of the floral receptacle, which is swollen and forms a ring round the ovary; their place of origin is always lower than the base of the ovary (see figs. 438 [2, 5, 7]). The pollen is adhesive. The fruit contains either few seeds or a single comparatively large seed.

The Discifloræ are in most instances woody plants, containing etherial oils and aromatic, resinous substances like turpentine. Amongst the Malpighiaceæ, Celastrineæ, and Ampelideæ are many lianes. The foliage-leaves are undivided in Erythroxylaceæ and Celastrineæ (see fig. 438 [1]), lobed in most Aceraceæ and Ampelideæ, and variously segmented and compounded in the other families (see fig. 438 [3]). The petals are usually small, and of a greenish-yellow colour. The filaments in Melianthaceæ and Aurantiaceæ are connate all together, or in groups. The fruits are extremely various. In Staphyleaceæ and Diosmaceæ they are follicles; in Celastraceæ and Rutaceæ, capsules (see fig. 325 [6], p. 431); in Zygophyllaceæ, Aceraceæ, and Malpighiaceæ, schizocarps; in the Tree of Heaven, of the family Simarubaceæ, winged achenes (samaras, see fig. 323 [7], p. 428); and in Ampelideæ and Aurantiaceæ, berries. The Discifloræ are distributed over the whole earth. The majority belong to the tropics, and several, *e.g.* Burseraceæ, Ochnaceæ, and Malpighiaceæ are exclusively tropical. The Diosmaceæ are confined to South Africa, the Rutaceæ to the districts of the Mediterranean and the Black Sea. Comparatively few species occur in the Northern Temperate Zone, or in corresponding situations on mountains. The Mountain Maple covers about the

Fig. 438.—Discifloræ.

1 *Euonymus Europæus* (Family Celastrineæ), flowering branch. 2 Longitudinal section through a flower. 3 *Quassia amara* (Family Simarubaceæ), flowering branch. 4 Gynæceum and floral receptacle. 5 *Ochna* (Family Ochnaceæ), receptacle, gynæceum, and one stamen. 6 Fruit of same. 7 Longitudinal section through the flower of the Tree of Heaven (*Ailanthus*, family Simarubaceæ). (Partly after Baillon.)

same ground as the Beech, and, in the Central Alps, even extends beyond the upper limit of the Beech. Fossil remains are found in the Mesozoic and Tertiary strata. The number of known species now living is about 9000.

Alliance LVII.—Crateranthæ.

Families: *Leguminosæ, Rosaceæ, Saxifragaceæ, Escalloniaceæ, Cephalotaceæ, Francoaceæ, Crassulaceæ, Hydrangeaceæ, Ribesaceæ, Philadelphaceæ, Styracaceæ, Hamamelidaceæ, Rhamnaceæ.*

Annual and perennial herbs, shrubs, and trees. Flowers abundant; actinomorphic and zygomorphic; hermaphrodite, pseudo-hermaphrodite, monœcious, and dicœcious. Floral-leaves in two 4–5-merous whorls, the lower whorl a calyx, the upper a corolla. Both whorls spring from the pitcher-shaped, bowl-shaped, or flat hypanthium, the petals always from the edge, the sepals, in part, also from the base of the hypanthium. In the last case the tube of the calyx is adnate to the external surface of the hypanthium. The gynæceum is in the middle of the hypanthium, and consists either of a single carpel with a unilocular ovary (see figs. 438*[1,3,4]), or of several separate unilocular carpels (see fig. 438*[2], and p. 74, fig. 208[2]), or of 2–many united carpels inclosing a multilocular ovary which may be adnate to the surrounding hypanthium at the base only, or from the base to the middle, or from the base to the top (see p. 74, fig. 208[4, 5, 6]). The ovules are situated on the ventral suture, and therefore in the inner angles of the loculi. The stamens spring from the edge of the hypanthium (see fig. 438*), and are in 1–2 whorls of 3–5 members each. The fruit is very various (pod, follicle, drupe, nut, berry, &c.), and the diversity in this respect affords the best means of distinguishing the numerous families belonging to this alliance. The hypanthium also varies considerably, and

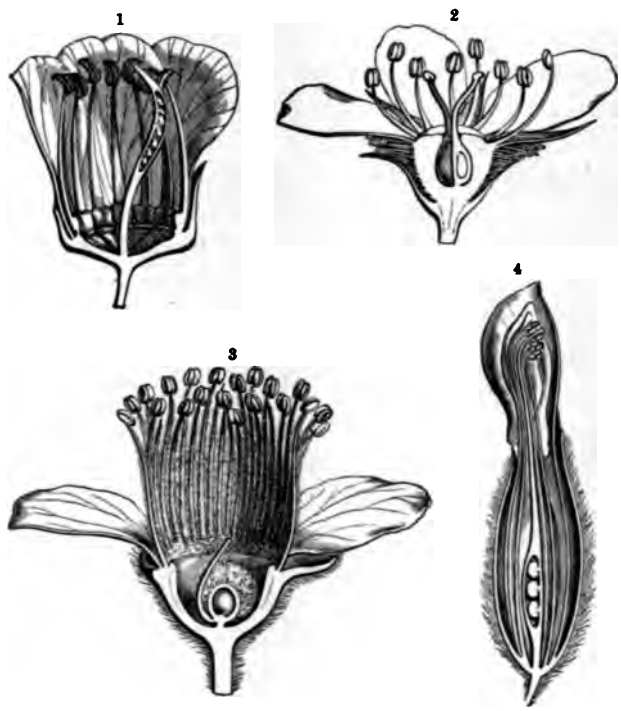


Fig. 438*.—Crateranthæ.

Longitudinal sections through the flowers of: [1] *Cadia varia* (Family Leguminosæ, division Cæsalpineæ). [2] *Agrimonia Eupatorium* (Family Rosaceæ, division Agrimoniaceæ). [3] *Chrysobalanus* (Family Rosaceæ, division Chrysobalanaceæ). [4] *Anthyllis Vulneraria* (Family Leguminosæ, division Papilionaceæ). (After Baillon.)

the families above enumerated may be placed in several groups according to the form of that structure. In the first group the hypanthium is short as compared with the floral-leaves, and dries up or detaches itself when the fruit is ripe (Papilionaceæ, Cæsalpineæ, Mimoseæ, Amygdaleæ, Rhamnaceæ); the pistil is simple. In the second group the hypanthium is flat, and bears the floral-leaves and stamens on its margin, and several separate unilocular carpels arranged in spirals in the middle of its surface; it does not fall off when the fruit ripens. In the third group the hypanthium undergoes further growth when the fruit ripens, and is converted into an envelope surrounding the nut-fruits, which have developed from the separate carpels in the interior of the pitcher-shaped cavity of the hypanthium (Agrimoneæ, Roseæ; see fig. 438*2, and fig. 208 1, 2, p. 74). In the fourth group the multilocular pistil is adnate to the hypanthium which surrounds it entirely, and is converted into a fleshy pericarp (Pomaceæ; see fig. 208 4, 5, 6, p. 74). In the fifth group only the lower half of the 2-carpellary gynæceum is adnate to the hypanthium, so that its upper half projects above the hypanthium, which is clothed by the calyx-tube (some of the Saxifragaceæ). In the sixth and last group the short hypanthium is only adnate at the base to the multicarpellary, actinomorphic gynæceum (Crassulaceæ, Styracaceæ, &c.). These groups are by no means sharply defined, and the links connecting them are again described as special families. It is also worthy of note that honey-secreting tissues in the flowers exhibit extreme variety of form and position; sometimes they constitute a fleshy lining to the inner, *i.e.* the upper-surface of the hypanthium (several Dryadeæ), sometimes a swelling round the base of the ovary (several Saxifragaceæ), sometimes an annular ridge, or a group of separate wart-like glands, which are seated on the edge of the extremely short hypanthium, and are looked upon as metamorphosed stamens (Crassulaceæ).

Amongst Cæsalpineæ, Pomaceæ, and Hamamelidaceæ are many species of arboreal growth, and amongst Mimoseæ, Amygdaleæ, Roseæ, Spiræeæ, Rhamnaceæ, and Hydrangeaceæ are large numbers of shrubs and under-shrubs. The majority of the herbaceous plants of this alliance occur in the families of Papilionaceæ, Dryadeæ, Agrimoneæ, and Saxifragaceæ. The Cæsalpineæ include several climbing lianes, the Papilionaceæ afford numbers of instances of switch-shrubs, and the Mimoseæ exhibit many shrubs with phyllodes. Amongst the Saxifragaceæ and Crassulaceæ many species with thick leaves (see vol. i. p. 327) occur. *Cephalotus* is insectivorous (see vol. i. p. 131). Compound pinnate or digitate foliage-leaves occur especially in Rubeæ, Dryadeæ, Roseæ, Papilionaceæ, Cæsalpineæ, and Mimoseæ (see vol. i. p. 533), whilst entire foliage-leaves are found particularly in Amygdaleæ, Styracaceæ, Crassulaceæ, Philadelphaceæ, and Rhamnaceæ. The flowers of Papilionaceæ and Cæsalpineæ, and of some of the Saxifragaceæ and Chrysobalaneæ, are zygomorphic; those of the other families are actinomorphic. In some Mimoseæ, Crassulaceæ, and Styracaceæ the petals are connate at the base. Small, inconspicuous, greenish petals are exhibited by some Agrimoneæ, Dryadeæ, Saxifragaceæ, Crassulaceæ, and by many Hamamelidaceæ and Rhamnaceæ; but most of the species of the alliance Crateranthæ have brightly-coloured petals. Dusty pollen has

only been observed in a very few species (e.g. *Poterium*). In some Dryadaceæ and Chrysobalaneæ the style springs in a curious manner from the base of the ovary (see fig. 438*[3]). The fruit is a pod (legume) in Papilionaceæ, Cæsalpineæ, and Mimoseæ, and these three sub-families are hence often classed together by botanists under the name of Leguminosæ. The fruit of Amygdaleæ, Chrysobalaneæ and Rubeæ is a 1-stoned drupe, that of Rhamnaceæ a 3-stoned drupe. The Agrimoneæ and Dryadeæ are distinguished by small nut-like fruits, and the Spiræeæ, Saxifragaceæ, and Crassulaceæ have follicles which dehisce at the upper part of the ventral suture. In most of the families above enumerated the seeds contain no endosperm; on the other hand, the thick cotyledons are crammed with reserve materials, and several of these seeds are used as important articles of human food (*e.g.* beans, peas, lentils, &c.).

The Crateranthæ are distributed in all quarters of the globe and in all latitudes. Cæsalpineæ and Chrysobalaneæ belong chiefly to the tropics, whilst Dryadeæ and Saxifragaceæ live principally in the arctic regions and on high mountains. The Papilionaceæ are found most abundantly in the area of the Mediterranean flora and in the steppes in the south-west of Asia. More than 800 species of the genus *Astragalus* alone are known to exist in the last-mentioned districts. The Mimoseæ, especially the species of the genus *Acacia*, are represented in Africa and Australia by many characteristic forms. Roseæ and Rubeæ, *e.g.* the genera *Rosa* and *Rubus*, occur in an astonishing variety of species in Central Europe, whilst the Spiræeæ and Amygdaleæ are in like abundance in the west of Asia. Crassulaceæ are most abundant at the Cape and in Mexico, but they are also represented by a great number of species of the genus *Sempervivum* in the mountainous parts of Southern Europe. *Rhodiola rosea*, which belongs to this family, occurs in the arctic flora, and *Sedum repens* is found in the Alps at a height of 3000 metres above the sea. Of the Saxifragaceæ, *Saxifraga oppositifolia* reaches the furthest north, it having been met with at the northernmost spot hitherto visited in Franz Joseph's Land, at 81° N. Lat. In the Central Alps this Saxifrage is found at an elevation of 3160 metres. Fossil remains of Rosaceæ, Leguminosæ, and Rhamnaceæ have been identified in the deposits of the Tertiary Period. The number of extant species hitherto discovered amounts to about 10,000.

Alliance LVIII.—Myrtales.

Families: *Myrtaceæ, Granataceæ, Onagraceæ.*

Annual and perennial herbs, shrubs, and trees, with entire foliage-leaves. Venation consisting of a main axial strand, with sinuous lateral strands branching pinnately from it. Flowers hermaphrodite, actinomorphic or zygomorphic. The floral-leaves spring from an annular or tubular hypanthium, which is fused with the inferior ovary; they are differentiated into calyx and corolla, each of which consists of a 2–6-merous whorl. The stamens are in 1, 2, or more whorls of 2–6 members

each, and spring from the fleshy annular or tubular hypanthium which rises up above the ovary. The fruit is baccate, drupaceous, or capsular.

The Granataceæ and Onagraceæ contain watery juices, whilst the species belonging to the other families are more or less rich in aromatic substances and etherial oils. Several are used as spices. Allspice is derived from *Pimenta officinalis*, and cloves are prepared from the flower-buds of *Eugenia caryophyllata*. The Circæeæ are small and delicate herbs, the Chamælauceæ are dwarf shrubs; whilst the genus *Eucalyptus* of the family Myrtaceæ includes several species which are amongst the highest trees in the world (see vol. i. p. 723). The flower in *Circæa* exhibits two sepals, two petals, and two stamens in order (see fig. 261[8], p. 236). In *Œnothera* and *Epilobium* the calyx and the corolla are composed of one 4-partite whorl each, and the andrœcium of 2 such whorls (see fig. 281, p. 282, and fig. 300, p. 354). In *Eucalyptus*, *Myrtus*, and many other genera the number of stamens amounts to over

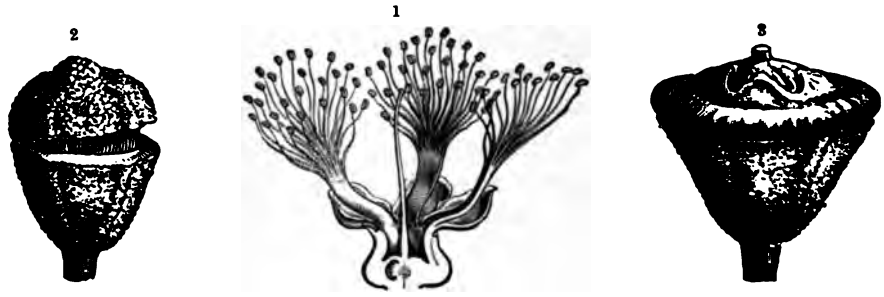


Fig. 439.—Myrtales.

[1] *Calothamnus*. Longitudinal section through the flower. [2] Flower-bud of *Eucalyptus globulus*, the connate sepals are detached from the receptacle as a lid when the bud opens. [3] Fruit of *Eucalyptus globulus*. (After Baillon.)

100; in *Calothamnus* (see fig. 284[4], p. 292) the stamens are coherent in bunches. Where the petals are suppressed, the filiform filaments are white or bright red and yellow. In the Fuchsias the sepals are coloured like petals; in some species of the genus *Eucalyptus* the sepals, which are joined together so as to form a lid, become detached from the floral receptacle before the flower opens. This remarkable phenomenon is shown in fig. 439[2]. The hypanthium which invests the ovary exhibits every possible transition in form, from a shallow saucer to a long tube (see fig. 266, p. 247). The ovary is in several families divided by septa, composed of tissue pertaining to the receptacle, which extend from the central column to the wall of the ovary. In Granataceæ (*Punica Granatum*) the ovary is in addition divided by a plate of tissue into an upper and a lower story, and placentas are developed in the chambers of both stories. The fruits of several Lecythidaceæ, *e.g.* those of *Lecythis*, open with a lid; those of *Eucalyptus* are in the form of hard woody capsules, which dehisce at the top by means of valves, pores, or slits (see fig. 439[3]). The fruits of *Circæa* are indehiscent; those of *Epilobium*, &c., are capsular, and open by valves. Many Myrtaceæ and the Fuchsias have baccate fruits. The fruit of the Pomegranate (*Punica Granatum*) resembles an apple. The seeds of *Bertholletia excelsa* of the family Lecythidaceæ are known as Brazil nuts, and have a coat as hard as stone;

those of the Pomegranate have a fleshy coat, and those of *Epilobium* are furnished with hairs. The Myrtales are distributed over all quarters of the globe. The Chamælaucese and Leptospermacese are natives of Australia and the islands of the Pacific Ocean. Several species of this family help to form Australian bush, whilst others, especially species of the genus *Eucalyptus*, constitute entire forests of great area. The Lecythidacese grow chiefly in South America. The Myrtacese are most abundant in America, and occur also in Asia and Africa. Europe only possesses one species, *Myrtus communis*, which belongs to the Mediterranean Flora. The Fuchsias are indigenous to Central and South America. The Epilobiums and

Fig. 440.—Melastomacese.

Melastoma Malabathricum. (After Baillon.)

Circæas live principally in the North Temperate Zone, and some species of the genus *Epilobium* occur in the arctic regions and on mountain heights. Fossil remains of Myrtacese and Granatacese have been found in the strata of the Tertiary Period. The number of species ascertained to exist at the present day is about 2500.

Alliance LIX.—Melastomales.

Family: *Melastomacese.*

Perennial herbs, shrubs, and trees, with opposite or whorled foliage-leaves. Leaves entire, with 3–11 curved ribs connected by transverse anastomoses (see fig. 440). Flowers hermaphrodite or pseudo-hermaphrodite; slightly zygomorphic. Floral-leaves differentiated into calyx and corolla. The bowl-shaped or tubular

receptacle is covered externally by the tube of the 4–6-sepalous calyx, is surmounted by the segments of the calyx-limb, and bears upon it the 4–6 petals which alternate with those segments. The gynæceum is composed of 3–8 connate carpels. The 3–8-locular ovary is adnate to the hollowed receptacle at the base only, or from the base to the middle, or from the base to the top. An axis rises up in the middle of the ovary and bears the placentas, which project into the separate loculi. The androecium is composed of 1–2 whorls of 4–5 stamens each. At the base of each anther is a spur-like appendage; dehiscence is apical by 1 or 2 small holes (see fig. 216[13], p. 91). The pollen is powdery. The fruit is a berry or a capsule which dehisces by valves. The seeds contain no endosperm.

The Melastomales belong chiefly to tropical America. Fossil remains have not been identified with certainty. The number of species ascertained to exist at the present time is about 2000.

Alliance LX.—Lythrales.

Families: *Lythraceæ*, *Cupheaceæ*, and *Lagerstrœmiaceæ*.

Annual or perennial herbs, shrubs, and trees with opposite or whorled foliage-leaves. Laminæ entire, with pinnate venation. Flowers hermaphrodite, actinomorphic or zygomorphic, with calyx and corolla. The cup-shaped or tubular receptacle is covered externally by the tube of the 3–16-sepalous calyx, the segments of which project beyond it and alternate with the 3–16 petals which are borne upon the receptacle. The gynæceum is composed of 2–6 connate carpels. The 2–6-locular ovary is free, and is situated at the bottom of the hollow receptacle. An axial column rises up in the middle of the ovary and bears the placentas, which project into the separate loculi. The androecium is composed of 1–2 whorls of 3–16 stamens each. The anthers have no appendages, and dehisce by longitudinal slits. The pollen is adhesive. The fruit is a capsule coated by the cup-shaped receptacle. The seeds contain no endosperm.

The Lythrales are distributed in all quarters of the globe. They exhibit greatest variety in tropical America. In the North Temperate Zone they are represented by the genera *Lythrum*, *Peplis*, and *Didiplis*. No fossil remains are known. The number of identified species now living is about 400.

Alliance LXI.—Hygrobiæ.

Families: *Hippuridaceæ*, *Callitrichaceæ*, *Myriophyllaceæ*, *Gunneraceæ*, *Trapaceæ*

Herbs and under-shrubs living in water or in wet places. Flowers hermaphrodite, pseudo-hermaphrodite, monœcious, and dicecious; actinomorphic. Floral-leaves inconspicuous, in 1–2 whorls of 2–4 leaves each. Gynæceum of one carpel or 2–4 connate carpels. The under half or the whole of the 1–4-locular ovary is adnate to the sepals, which cohere so as to form a cup. Each loculus contains one ovule in its inner angle. The androecium is composed of 1–8 stamens. The fruit is

a schizocarp (*Callitriche*; see p. 427, figs. 322[3] and 322[4]) or a drupe covered with a thin coat of pulp; it becomes detached from the receptacle. In the Water Chestnut (*Trapa natans*; see vol. i. p. 607, fig. 144) the two whorls of two sepals each which are adnate to the ovary become a part of the fruit, and their apices project in the form of four stiff points. The Hygrobiæ are distributed in every quarter of the globe, but belong especially to the North Temperate Zone. The Gunneraceæ inhabit the Southern Hemisphere. Fossil remains of a plant resembling *Myriophyllum* have been found in strata of the Tertiary Period. The number of extant species known is about 100.

Alliance LXII.—Passiflorales.

Families: *Passifloraceæ, Loasaceæ, Datiscaceæ, Samydaceæ, Turneraceæ, Papayaceæ.*

Annual or perennial herbs, shrubs, and trees, with palmately-lobed foliage-leaves. Venation palmate (radiating). Flowers hermaphrodite or pseudo-hermaphrodite, and dicœcious; actinomorphic. The floral-leaves spring from a cup-shaped hypanthium in one or two 4–5-merous whorls. The gynæceum is composed of 3 connate carpels. The unilocular ovary is free, and is raised upon a more or less elongated stalk from the bottom of the receptacle, or else it is sessile and adnate to the cup-shaped receptacle either half-way from the base or from base to top. The ovules are borne upon three placentas which project in the form of cushions from the internal wall of the ovary. The androecium is composed of 4–5 stamens which spring from the edge of the cup-shaped hypanthium. The fruit is a berry or a capsule opening by valves. The seeds contain a fleshy endosperm, in which is imbedded a straight embryo.

The Datiscaceæ have a sepaloid perianth. In the Loasaceæ and Passifloraceæ the floral-leaves are in two whorls, both of which are petaloid. In the Passifloraceæ a many-membered corona is inserted between the androecium and the petals. The Passiflorales belong chiefly to tropical America. Fossil remains have not been identified with certainty. The number of extant species known is about 700.

Alliance LXIII.—Pepones.

Families: *Cucurbitaceæ* and *Begoniaceæ.*

Annual and perennial herbs and under-shrubs (suffrutices). Venation of the foliage-leaves radiating (palmate). Flowers solitary or in cymes; actinomorphic; pseudo-hermaphrodite, moncecious and dicœcious. The uppermost part of the receptacle, which is deeply hollowed, is developed as a hypanthium, and from it spring the floral-leaves in 1–2 whorls of 2–5 segments each. When two whorls are present they are either both petaloid in colour or the under whorl is a calyx and the upper a corolla. The petals are either free or partially coherent. The ovary is inferior. The ovules are borne on thick pads which are split in two longitudinally,

and project into the middle of the ovary. The andrœcium is composed of 5 or many stamens which spring from the hypanthium, and are joined at the base to the corolla. The fruit is baccate or capsular. The seeds contain no endosperm.

The Cucurbitaceæ have symmetrical foliage-leaves—no stipules, but often tendrils (see vol. i. p. 696, fig. 165); the Begoniaceæ have oblique, unsymmetrical laminæ, large lacerated stipules, and no tendrils (see vol. i. p. 420, fig. 110 [1]). The whorls of floral-leaves are 5-merous in Cucurbitaceæ; in Begoniaceæ the floral-leaves of the female flowers are arranged in two whorls of 3–5 segments each, and those of the male flowers in two whorls of 2–5 segments each. Three winged ridges project from the inferior ovary in Begoniaceæ. The stalks of the ovules of Cucurbitaceæ fill the cavity of the ovary so completely that only small interstices are left between them. In many Cucurbitaceæ these stalks are converted when the seeds ripen into a succulent mass (*e.g.* in cucumbers, melons, and gourds). In Begoniaceæ also they project from the walls into the middle of the ovary, and the latter looks in consequence as if it were divided into loculi. The andrœcium exhibits great diversity. In some Cucurbitaceæ the five stamens are free; in others they are partially united, and in a third group they are all completely fused together into a column. In Begoniaceæ, also, the stamens are connate and form a column. In many cases the anthers are sinuous, and in the genus (*Cyclanthera*) there is a continuous anther all round the column. The Pepones are mainly tropical plants. The Begoniaceæ grow especially in the tropical forests of America, where they are not infrequently epiphytic. There is still some doubt as to the place of origin of Melons, Gourds, and Cucumbers. The alliance is represented by the Squirting Cucumber (*Elaterium*) in the South of Europe, and by Bryony (*Bryonia*) in Central and Northern Europe. No fossil remains have been discovered. The number of extant species hitherto identified is about 1100.

Alliance LXIV.—Cactales.

Families: *Opuntiaceæ* and *Cactaceæ*.

Perennial plants, whose stems are much swollen or flattened. Flowers solitary; actinomorphic or zygomorphic; hermaphrodite. The ovary consists of a hollow, cup-shaped floral receptacle, from the inner wall of which spring filiform stalks bearing the ovules (see fig. 209 [1, 2], p. 77). The external surface of the receptacle is clothed by floral-leaves arranged in a spiral; the lower leaves are small and inconspicuous, the upper petaloid and brightly coloured (see figs. 441 [1, 2, 3, 4, 5]). Inside the upper tubular prolongation of the receptacle are crowds of stamens arranged spirally. The pollen is adhesive. The fruit is unilocular and succulent (see fig. 441 [2]). The seeds contain no endosperm.

The genus *Pereskia* alone exhibits thick, green foliage-leaves; in the other genera the leaves are replaced by small caducous scales or thorns, and assimilation is effected by means of the green cortical tissue of the swollen stems (see vol. i. pp. 327 and 440). The species of *Rhipsalis* and *Phyllocactus*, which are epiphytic

on the branches of old trees, have much-branched and segmented phylloclades, which often hang in curves; the segments of the stem in Opuntias are laterally compressed, and more or less discoid, resembling fleshy leaves. The cylindrical stems of the Queen of Night (*Cereus nycticalus*), already so frequently alluded to, are prismatic, and climb up rocks and the bark of trees by means of clinging roots. Other species of *Cereus*, such as *Cereus giganteus*, which grows to a height of 20 metres, possess erect columnar stems with candelabra-like ramifications. Another set of *Cereus*-species, including the many forms of *Mammillaria*, *Melocactus*, *Echinocactus*, and *Echinopsis*, are spherical or truncate; they are covered either with papillæ, each of which is crowned by a bunch of prickles (see fig. 441 [3]), or

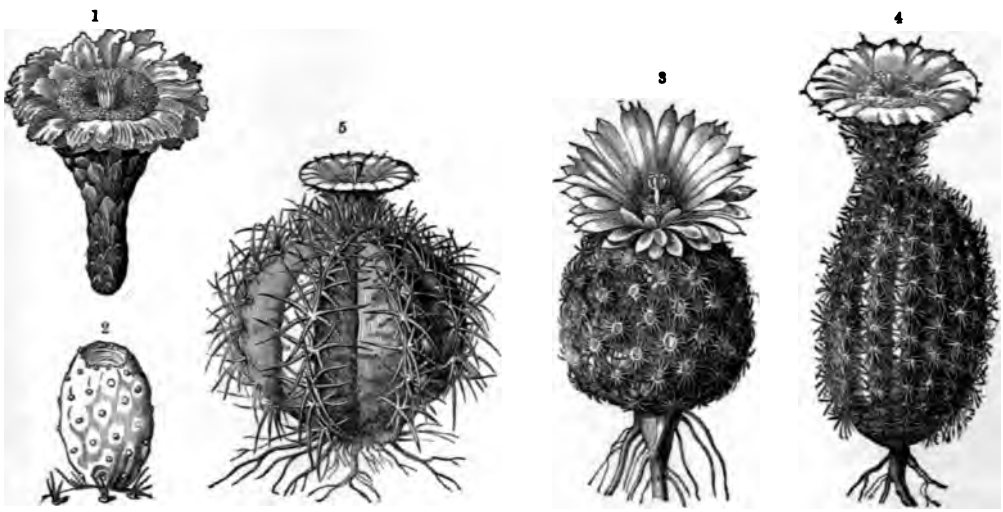


Fig. 441.—Cactaceæ.

[1] Flower. [2] Fruit of *Cereus giganteus*. [3] *Mammillaria vectinata*. [4] *Cereus dasyacanthus*. [5] *Echinocactus horizontalis*. All the figures reduced.

with tubercles, which coalesce into crests and ribs (see figs. 441 [4] and 441 [5]). The Cactuses are natives of the New World, and inhabit regions where a short, rainy season is followed by a prolonged period of drought. The largest number of species is found in Mexico. Some species also occur at high elevations in the Andes. No fossil remains are known. The number of species ascertained to exist at the present time is about 1300

Alliance LXV.—Ficoidales.

Families: *Portulaceæ*, *Molluginaceæ*, *Ficoidaceæ*, *Mesembryanthemaceæ*.

Annual and perennial herbs and under-shrubs, with entire fleshy foliage-leaves. Flowers solitary or in fascicles and glomerules; actinomorphic, hermaphrodite. The floral-leaves free or else connate at the base; in one, two, or several 2–5-merous whorls. Either all the floral-leaves, or only those of the lowest whorl, are sepaloid; in the latter case, the upper whorl or whorls are petaloid. The

gynæceum is composed of 3, 5, 8 or more connate carpels. The ovary is adnate to the bowl-shaped receptacle at the base only or as regards the lower half of its surface, or from the base to the top; it is crowned by a radiating stigma of 3–10 rays, and is uni- or multi-locular. A column rises up in the middle of the ovary, and bears the ovules. In the case of multilocular ovaries, the ovules are borne on ridges and strands which project from this column into the loculi. The androecium is composed of one or several whorls of 3–10 stamens each. The anthers have no spurs, and they dehisce by longitudinal slits. The pollen is adhesive. The fruit is a capsule or an achene. The seeds contain a mealy albumen and a curved embryo.

The Ficoidales chiefly inhabit dry localities. Only a few species (e.g. *Montia fontana*) live in water and on marshy soil. They are distributed all over the globe. Most of the Portulaceæ belong to South America and the Cape. The Mesembryanthemaceæ are developed in extraordinary variety in South Africa. There are over 300 species of the genus *Mesembryanthemum* alone at the Cape. No fossil remains are known. The number of extant species hitherto identified is about 500.

Alliance LXVI.—Umbellales.

Families: *Cornaceæ*, *Araliaceæ*, and *Umbelliferæ*.

Annual or perennial herbs, shrubs, and trees which flower profusely. Flowers in capitula, umbels, and cymes. Floral-leaves differentiated into calyx and corolla. The calyx 4–5 sepalous, with its tube clothing the inferior ovary and the limb represented by 4–5 small teeth, which surround the top of the ovary. The corolla is likewise 4–5 petalous, the petals free and alternating with the sepals. The gynæceum is composed of a whorl of connate carpels; ovary inferior, 2–5 locular. Every loculus corresponds to a carpel, and contains a single ovule, which is suspended near the upper end of the loculus (see fig. 442 [4]). On the top of the ovary is a glandular disc, which secretes honey (see figs. 442 [2, 4, 7]). The androecium consists of a whorl of 4–5 stamens. The stamens are quite separate, and stand in a circle round the honey-secreting disc. The fruit in Umbelliferæ is a schizocarp (see p. 427, fig. 322 [5, 6, 7] and fig. 442 [3]), in Cornaceæ and Araliaceæ a berry or drupe. The seed contains an abundant endosperm, in which the embryo is imbedded.

The Cornaceæ are for the most part woody plants, with entire, opposite foliage-leaves, possessing a venation of arched strands (see p. 231, fig. 260 and vol. i. p. 630). The Araliaceæ, of which the Ivy (*Hedera Helix*, see vol. i. p. 703, fig. 167) may be taken as a type, are woody plants with climbing roots, or shrubs and herbs with radiately-veined foliage, and the Umbelliferæ, which are very rich in aromatic substances, oils, and resins, are for the most part herbs whose stems in many species reach a length of 3–4 metres, as, for instance, in *Ferula communis* and *Euryangium Sumbul*. The foliage-leaves of Umbelliferæ are usually much divided (see fig. 442 [1]), those of *Hydrocotyle vulgaris*, a plant which lives in swamps, are peltate (see

fig. 442[5]). The calyx, corolla, and andrœcium are 4-merous in Cornaceæ, 5-merous in Umbelliferæ and Araliaceæ (see figs. 442[2] and 442[6], and p. 289, fig. 283[4]). The Umbellales belong chiefly to the North Temperate Zone, but the Araliaceæ are

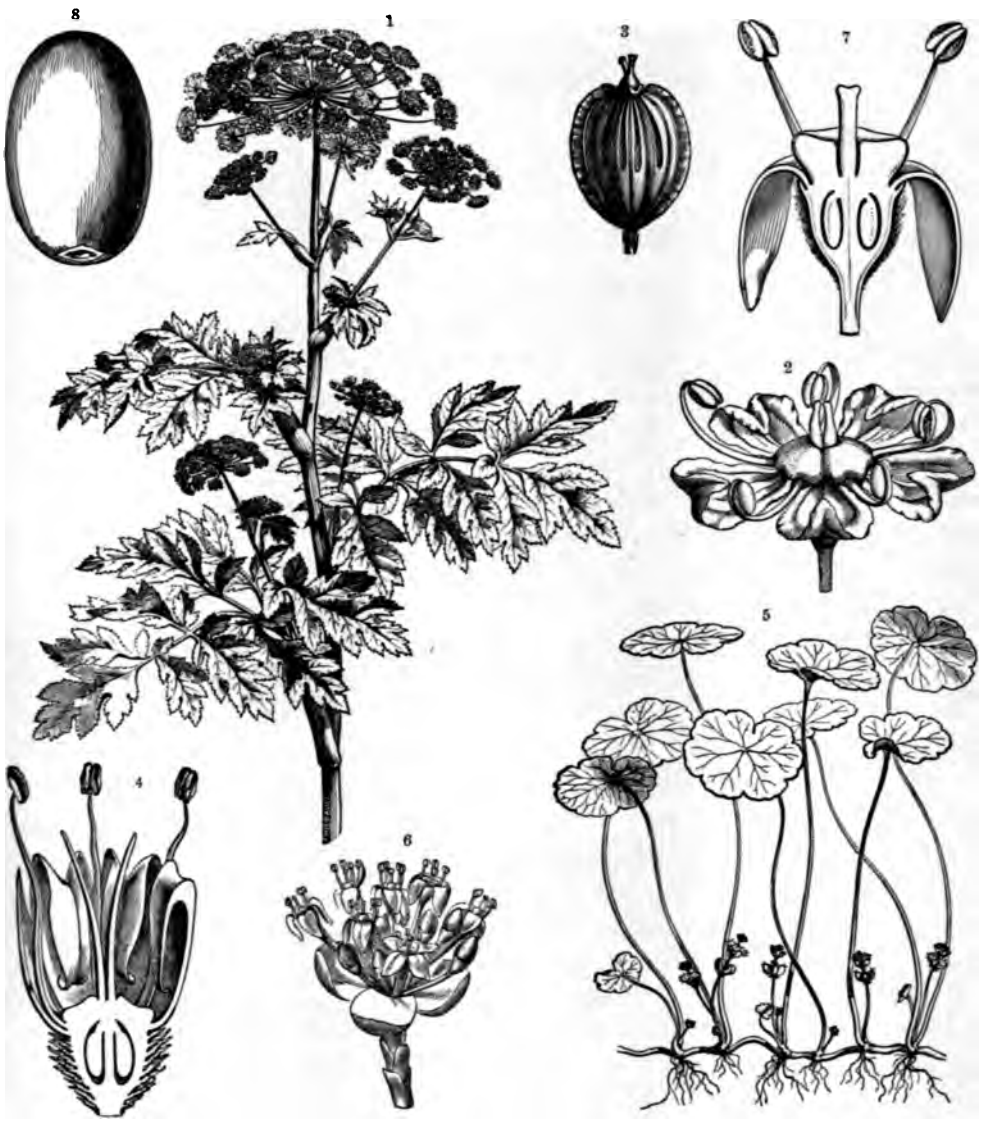


Fig. 442.—Umbellales.

[1] *Heracleum Sphondylium* (Family Umbelliferæ), flowering plant. [2] Single flower. [3] Fruit. [4] Longitudinal section through the flower of *Eryngium maritimum* (Family Umbelliferæ). [5] *Hydrocotyle vulgaris* (Family Umbelliferæ), entire plant. [6] *Cornus mas* (Family Cornaceæ), inflorescence. [7] Longitudinal section through a flower. [8] Fruit. [1] reduced; [2], [3], [4], [5], [6], [7], and [8] magnified. (After Baillon.)

also represented by a number of species in the Tropics. Several of the Umbelliferæ are natives of the arctic area of vegetation and of alpine regions. *Gaya simplex* occurs in the Central Alps as high as 2600 metres above the sea-level. Fossil remains, belonging chiefly to the families of Araliaceæ and Cornaceæ, have been

found in the deposits of the Mesozoic and Tertiary Periods. The number of extant species identified hitherto amounts to about 1800.

4.—THE DISTRIBUTION OF SPECIES.

Distribution of Species by Offshoots.—Distribution of Species by Fruits and Seeds.—Limits of Distribution.—Plant-Communities and Floras.

THE DISTRIBUTION OF SPECIES BY OFFSHOOTS.

When the dreaded Dry-rot spreads unhindered over the surfaces of wooden beams, in a dark, damp cellar, its mycelium presents quite a strange appearance. Grouped in a circle around a dark centre of dead, disintegrating, and crumbling wood are a number of white spots, joined by indistinct lines to a centre. But this was not always the case. That which now forms the dead and crumbling centre was formerly the seat of the first development of the mycelium, then composed of a coherent network of mycelial threads and appearing to the naked eye as a single rounded white spot. The mycelial threads then crept out like rays all round the periphery, and as the white spot increased in diameter its centre became proportionately dark. The mycelial threads forsook their first settlement; they died off, and the wood they had destroyed then appeared merely as the dark centre of a white ring. In consequence of its continual widening the ring at length becomes segregated into stars, and is gradually transformed into a wreath of isolated mycelia, or, in other words, a group of separate but distinct mycelial spots arranged in a circle arises from a single mycelium in consequence of its radiating method of growth.

The mycelium of Gasteromycetes, of many Fungi allied to Morels, and especially of many Agarics growing in the forest mould or in meadow humus, also exhibit under favourable conditions this ring and wreath formation. Although it is not possible to see the subterranean growth directly, its results are readily recognizable, since the receptacles rise above the ground from the separate portions of mycelium and indicate their distribution; these receptacles occur in regular circles, and when their colour contrasts with the surroundings they are especially conspicuous. Rings of this kind are shown in fig. 443 formed by the Ascomycete *Spathularia flavida*. The subterranean mycelium of this Fungus exercises no injurious influence on plants in the immediate neighbourhood—at any rate, the mosses, grasses, and weeds which compose the carpet of the meadow round about show no sign of weakness, but are equally fresh and luxuriant within and without the rings. But it is not so in meadows where Agarics of the genus *Marasmius* and others have settled. The meadow-plants whose roots and root-stocks have been penetrated by their mycelia die off, and the places can be easily recognized by the withering and discoloration of their green aërial parts. On first looking at these spots one might easily suppose that the foundations of old circular walls were lying close under the turf which had

Fig. 443.—Fairy Rings in a meadow near Trins in the Tyrol, formed by the ascomycetous fungus *Spathularia flavida*.

in consequence dried up above the stones; that this is not so may be readily proved by digging, and this shows us at the same time that the humus and roots in these places are quite riddled and wrapped round by the mycelium of the Fungi named. The brown and grey ring- and crescent-shaped stripes show up most clearly on meadows because a parallel stripe of a specially vivid green is usually seen close to them. The reason of this is that, after two years, new plants develop in all those places which were formerly occupied by the mycelium, and have been abandoned by it in its centrifugal growth. Strangely enough, these plants are not the same species which were killed there in the previous year, but are herbs and grasses which find a suitable nourishing soil in the places which have lain waste for 1–2 years. The roots and root-stocks of the plants killed by the mycelium have meanwhile decomposed, together with the remains of the mycelium and the receptacles of the Fungi. The soil is thus manured, and plants which usually settle on fallow ground grow there in abundance. They raise luxuriant stems and leaves, and thus is produced on the inner side of each bare stripe a parallel one of a bright green colour.

This phenomenon has long been noticed by country people, particularly in regions where pastures are an important feature. It is associated with the influence of ghosts, witches, and elves; hence the name of fairy rings. In Upper Austria these bare dry spots are regarded as the rendezvous of the witches, and Walpurgis Night (1st May) is supposed to be the time when they are produced. In the Tyrol and other primitive countries the most varied superstitions are held to account for these curious stripes and patches.

Fairy rings are sometimes formed by plants with underground rhizomes and runners, although not so frequently as by the subterranean mycelia of the Fungi named. Some Composites (for example *Petasites niveus* and *P. officinalis*, *Arnica Chamissonis*, *Achillea Millefolium*), Labiates (*Betonica grandiflora*, *Mentha alpigena*), Irises (*Iris arenaria* and *I. Pallasii*), Grasses, Sedges, and Rushes (*Hierochloa borealis*, *Sesleria cœrulea*, *Carex Schreberi*, *Juncus trifidus*), under suitable conditions of soil form ring-shaped and garland-like colonies independently of Fungi. The mode of growth in these plants is like that of the Dry-rot. Young plants grow up with closely crowded shoots; these then spread out on all sides, and the connecting links die off simultaneously. In this way the original settlement is left a bare patch with dried remains surrounded by a circle of distinct and vigorous offshoots. Though shoots are very numerous they still stand close together even after they have severed connection, and if their annual growth is but slight it is some time before an actual ring is formed. It is in this case, however, the more striking, so that even a casual passer-by cannot fail to notice it. This happens principally in the above-named Grass-like plants, and among them especially in *Sesleria cœrulea*, which has attained a certain celebrity in Sweden as the ring-forming plant. It is there popularly termed *elf dansar*, and legend has it that the elves are especially fond of holding their nightly dances on places where rings of this Grass have been formed.

Of course good rings are only produced by the plants named if the foremost buds produced by the subterranean internodes, *i.e.* those which form the terminations of the radiating stock or rhizome, undergo further development, while the intervening ones perish. This may not be the case under certain conditions, particularly if the growth of the terminal buds is retarded or stopped. For this reason fairy rings are formed much less frequently on stony, uneven ground than on flat homogeneous soils; and the best lands for this kind of fairy rings are pastures stretching over a mountain plateau, or the even floor of a valley.

If specimens of the plants here described are planted on smooth ground, in good soil in a garden, in places where there is no obstacle to their spreading, they will form the rings and wreaths in question within a few years. But in spite of this, very few people are ever able to witness this interesting spectacle in gardens, because gardeners will not leave the rings alone, regarding the bare patch in the centre as unsightly and that the existence of a ring is a slur upon their craftsmanship. I remember noticing this many years ago in the Botanic Gardens at Innsbruck. The perennial plants were cultivated in certain beds close together, and to each species was allotted a limited amount of space. When the spring came round the gardener dug up the periphery of the circle, and planted it in the centre, to catch the escaping plants, as he put it. In the spots where *Mentha alpigena* had stood the previous year only a few withered stumps were to be seen, and not a single living shoot could be found. But shoots with their tops above the ground could be seen in a circle in the neighbouring beds, and also in the paths between the beds all round the space set apart for this species of Mint. These shoots were ruthlessly dug up and planted again in the forsaken spot. Every year or every second year this capturing of the fugitives was repeated, not only in the case of the Mint, but in many other instances, as, for example, *Achillea asplenifolia* and *A. tomentosa*, *Betonica grandiflora*, and *Lysimachia thyrsiflora*.

Amongst aërial-sprouting plants which form rings and wreaths may be numbered the majority of Moulds, Lichens, and Mosses. The Mould, *Penicillium glaucum*, which settles on the fruit rind of oranges, apples, and pears, at first makes its appearance as a mere point, but later as a circular spot, and finally as a distinct ring surrounding a brown and rotten centre.

The most striking of the ring-forming Lichens are those which stand out from their substratum on account of their colour. Most noticeable in this respect are the white *Parmelia conspersa*, which contrasts with the dark slate rock, and the saffron-yellow species *Amphiloma callopisma* and *Gasparrinia elegans*. The gelatinous Lichens, dark olive-green normally, but black when dried, especially *Collema multifidum* and *C. pulposum*, often form such regular wreaths on a light background of limestone that they look as if they had been drawn with compasses, and the tiny yellowish-red *Physcia cirrochroa* has a particularly elegant appearance when it has radiated out from the hundreds of spots where it established itself on the flat surfaces of a steep calcareous rock. One might almost think that the small orange wreaths had been painted in with a brush. They also remind one of the fleecy

clouds in the evening sky, whose edges are reddened with the rays of the setting sun; and if I am not mistaken, this Lichen has obtained its name on account of this resemblance.

The chief Liverworts and Mosses which form rings and wreaths when they grow on the flat surfaces of steep rock-faces and on the bark of old tree-trunks, are *Frullania dilatata*, *Radula complanata*, *Amblystegium serpens*, *Anomodon viticulosus*, and *Hypnum Halleri*. When they first settle they are scarcely noticeable on account of their minuteness, but they spread very rapidly, their firmly adherent stems forking and radiating out in all directions, the whole plant at a little distance now forming a greenish-yellow spot of circular outline. While growth proceeds in this way round the periphery of the Moss-plant, covering the rock or bark like a carpet by the multiplication of its outer forked branches, the older parts near the original place of settlement become dry, disintegrate, and are blown away like dust by the wind, the naked rock or bare bark thus again coming into view. In this way 5, 10, or 20 new Moss-plants are derived from the original one, and stand in a circle round the bare centre. This circle widens from year to year, until at last it is interrupted by gaps, and then 20 or more specimens of the Moss are seen adhering to the substratum arranged in a circle more than a span from the original settling place.

In order that the ring or wreath arrangement of the offshoots above described should obtain, it is necessary that the original plant should dry up and decompose, and that the shoots which radiate from it should also die off behind in proportion as their growing points travel away from the centre of the settlement, and, finally, that no new ring-forming species should establish itself, or spread on the dead centre for a considerable time. These conditions are only comparatively rarely fulfilled, and this is the reason that ring and wreath formations are relatively so scarce.

It happens much more frequently that the plant forming the starting-point of a colony, after it has sent out creeping threads of cells, runners, shoots, and the like in all directions, does not itself perish, but remains living and active in the centre of its separated shoots, even sending out new shoots year after year. In the same way the separated shoots repeat the parent-method of growth, *i.e.* they send out shoots in all directions like the mother-plant, though perhaps less regularly, and thus of necessity some of the young shoots come back to the bare centre and settle down where the mother-plant originally stood. The following phenomenon may also be observed: A plant gives off annually a pair of horizontal shoots on one side only, let us say on the south; their buds in the course of time become independent plants, and each again sends out a few horizontal shoots towards the south. In a few years' time these offshoots give rise to 20–30 plants, which are more or less distant from the starting-point, according to the length of the shoots. In all these cases the offshoots are not arranged in a ring or wreath round an empty centre, but in lines or clusters.

Like the ring- and wreath-forming colonies, the offshoots, forming lines and clusters, may be underground or aërial. The receptacles of many Fungi emerge in a

clearly lineal arrangement from the mycelial threads running below the surface of the ground and in dead, rotten tree-trunks. Some Mosses form colonies in very regular lines from their rhizoids and horizontal underground protonemas. The most conspicuous, however, is the line formation produced by roots which run horizontally below the soil. The Aspen (*Populus tremula*), the Sea Buckthorn (*Hippophae rhamnoides*), *Lycium barbarum*, the Raspberry (*Rubus Idæus*), the Dwarf Elder (*Sambucus Ebulus*), *Asclepias Cornuti*, various species of *Linaria* and *Euphorbia*, and numerous other plants (*cf.* p. 27) produce special horizontal underground roots, which give off buds towards the upper side. The shoots arising from these buds form separate independent plants after the root which formed them has died away. Obviously the plants follow the direction of the roots, and are arranged in rows. Even for years afterwards the line-like arrangement of the individuals in such colonies can still be recognized. When the bud-forming roots are of considerable length, the terminal offshoots are sometimes situated at some distance from the mother-plant. I saw single offshoots from the root of an Aspen push up through the ground 30 paces from the woody parent stem. Stems of *Asclepias Cornuti* spring up from the thick horizontal roots deep under the ground, at intervals of about 40 cm., and in them also can the linear arrangement be sometimes very clearly seen. When the individual offshoots in their turn give rise to horizontal roots, the line-formation is lost sight of more and more, and a scattered group spread over a wide area is the result. Sometimes the older portions of the colony die off completely, and as the individuals in one direction disappear, those in the other grow more luxuriantly. One might almost suppose the whole group to have taken a few steps forwards. This phenomenon can be seen particularly well in Raspberry bushes. On suitable soil a group of Raspberries will move about 2 paces every year, and therefore, after 10 years, they may have moved about 20 paces. If Raspberry bushes are planted near an inclosed piece of ground along a fence or hedge, it may happen that ten years later not a single one can be seen in the original place, while on the other side of the fence, in the neighbouring piece of ground, quite an assemblage of Raspberry plants has come into existence.

The clustered or linear colonies which spring from underground tubers have the following very simple history. After a tuber has been fully formed on the underground shoot of a plant the slender bridge-like connections which have hitherto served for the conduction of food break down by the decay and decomposition of their tissues. The new tubers thus separated from the mother-plant send out stems from their buds, after the necessary period of rest these push up above the ground and also give rise to new subterranean shoots with tuberous swellings. These fresh tubers, after they have become disconnected, again form the starting-points for tuber-forming plants. This goes on until after a few years the soil all round the place where the first tuber had been is crowded with hundreds of separate tubers, and corresponding to these above the ground is a group of hundreds of separate leafy stalks. It depends of course on the number and length of the underground tuber-forming shoots whether the group is crowded or scattered. In the Artichoke

(*Helianthus tuberosus*) the tuber-forming shoots are short; the colony is therefore crowded, and only spreads slowly over a larger area. The Alpine Enchanter's Nightshade (*Circæa alpina*; see fig. 444[3]) forms elongated tubers at the end of shoots 6 cm. in length, about 5 of them round the mother-plant, whilst each of the new plants arising from these tubers repeats this formation in the same colony. Since 6 cm. is a considerable length compared with the size of the Enchanter's Nightshade, the group is scattered and in a few years extends over a considerable area. The tuber formation of *Thladiantha dubia*, a gourd-like plant growing in

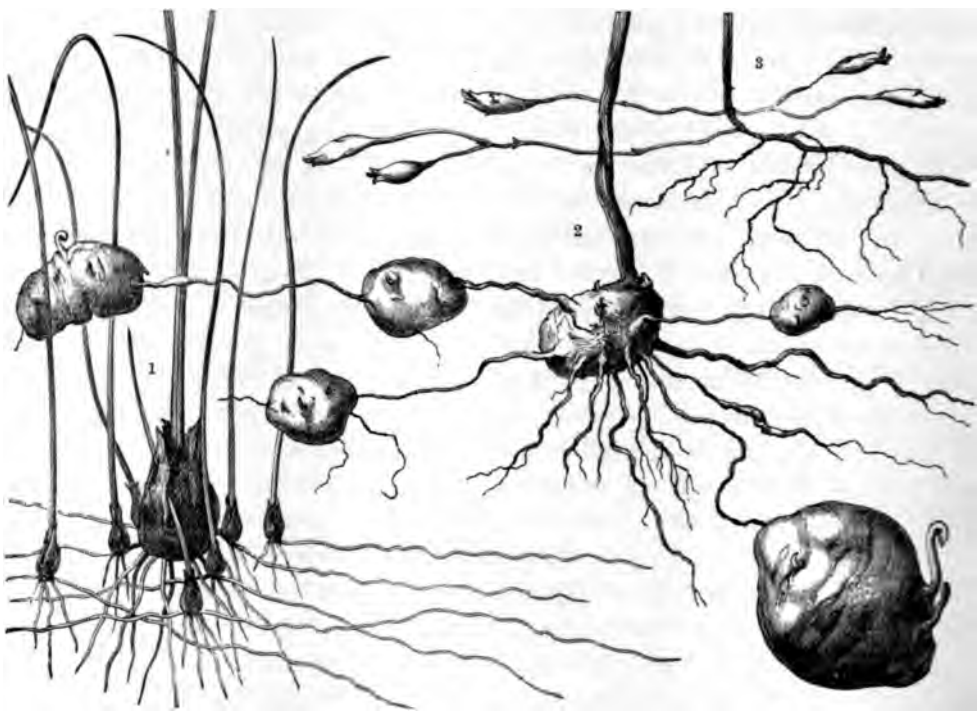


Fig. 444.—Plants with tubers and bulbs whose mode of growth leads to the formation of colonies arranged in lines and clusters. [1] *Muscari racemosum*. [2] *Thladiantha dubia*. [3] *Circæa alpina*.

Eastern Asia, is especially luxuriant; its shoot-formation is shown in fig. 444[2]. In this plant a whole series of tubers which are chained together by thin threads 4–8 cm. long is formed on each shoot. Usually they form series of 5–10, and such a chain is about 50 cm. long. As a new plant grows from each tuber and again produces chains of underground tubers, the *Thladiantha* in a few years may occupy an area of 10 sq. metres, and will form a cluster which is both crowded and rapidly increasing in circumference. A further excellent example of the same thing is *Glaux maritima* which often spreads in the most diagrammatic manner in bare sandy places near the sea-shore.

Many tuber-forming plants producing clustered colonies inhabit marshes, especially such as are liable to great alteration in the level of the water and are exposed in years of drought to the danger of temporarily drying up. Many Pond-

weeds (*Potamogeton*), e.g. *Potamogeton pectinatus*, form a large number of small tubercles on their shoots which creep horizontally through the mud: *Scirpus tuberosus*, like the Alpine Enchanter's Nightshade, forms underground shoots 10–15 cm. in length, each terminating in a tuber as large as a chestnut, and since the plants to which these tubers give rise themselves repeat this formation of offshoots, the diameter of the clustered colony increases about 20–30 cm. every year. The Arrow-head (*Sagittaria sagittifolia*) also develops peculiar tubers. In the autumn, offshoots whose scale-leaves terminate in a sharp point not unlike those of the Couch-grass spring from the knotty stems hidden in the mud. The leaf which envelops the swollen end of the offshoot has a stiff point and plays the part of an earth-borer or rather of a mud-borer, since it makes a path for the offshoot which may elongate as much as 25 cm. The swollen end of the offshoot, which is about the size of a hazel-nut, bears a small bud with greenish, closely-folded leaves, and this, together with its tuberous support, remains alive during the winter, while the plant to which the offshoots owed their origin perishes. In the following spring each of the small buds grows up into a new plant at the expense of the reserve-materials stored in the tuber, and now instead of the old dead plant we have a small group of young independent plants rising from the mud.

The colonies of offshoots arranged in lines and clusters, which are developed from underground rhizomes and shoots, elongate horizontally, and form buds laterally and at their growing point, and in the same proportion as they fork and divide in front they die off behind, so that the individual sprouts become separated. To this category belong several species of *Dentaria*, *Anemone*, Couch-grass (*Agropyrum*), Mint (*Mentha*), Yarrow (*Achillea*), Willow-herb (*Epilobium*), Butterbur (*Petasites*), and the Woodruff (*Asperula odorata*). The length of the underground shoots which form the buds in these plants is very varied, as will be clearly seen from the table we insert here.

	Centimetres.		Centimetres.		Centimetres.
Anemone ranunculoides	5–10	*Epimedium alpinum*	15–20	*Hierochloa borealis*	35–45
Monarda fistulosa		*Silene alpestris*		*Urtica dioica*	
Melissa officinalis		*Mentha viridis*		*Carex pilosa*	
Origanum vulgare		*Asperula odorata*	20–25	*Glaux maritima*	45–55
Achillea Millefolium	10–15	*Mentha piperita*		*Arnica Chamissonis*	
Equisetum arvense		*Rubia tinctorum*		*Daphne Philippi*	
Asperula taurina		*Senecio Fuchsii*		*Senecio fluviatilis*	55–60
Oxalis corniculata		*Mercurialis perennis*	25–30	*Tussilago Farfara*	60–75
Betonica grandiflora		*Mentha crispa*		*Solidago canadensis*	
Tanacetum Balsamita		*Agropyrum repens*		*Petasites niveus*	75–85
Aster salignus		*Ægopodium Podagraria*		*Mentha alpigena*	
Dentaria glandulosa	15–20	*Convolvulus arvensis*	30–35	*Nardosmia fragrans*	85–100
Carex arenaria		*Saponaria officinalis*		*Epilobium angustifolium*	
Juncus arcticus		*Potentilla bifurca*	35–45	*Petasites officinalis*	100–150

These numbers do not represent the lengths of single internodes, but those of the whole annual underground shoots which may consist of many internodes. For example, the year's underground shoot of the Umbellifer *Ægopodium Podagraria* has 8 internodes, of which the proximal one is the longest and the distal the shortest.

The rapidity of the extension and the dimension of the colonies which are produced from rhizomes and runners depends upon the length of the annual shoot, and upon whether or not the soil is favourable to the spreading of the offshoots, just as it does in the linear or clustered colonies arising from underground roots and tubers. In wood-clearings and on the banks of rivers many of these plants develop in a surprisingly short time, as, for example, *Calamagrostis Epigeios*, *Epilobium angustifolium*, the North American Golden Rod and Rudbeckias (*Solidago Canadensis* and *Rudbeckia laciniata*), and these also have the property of suppressing and destroying all other vegetation in places where they have taken possession. This fact is turned to practical account by farmers who use certain Grasses which form linear and clustered offshoots to bind together loose soil, especially river sand. But there are also plants in this category which are veritable plagues to the farmer, the establishment and propagation of which he opposes by every means in his power. Examples of these dreaded plants, which, when they establish themselves in the fields and garden-beds, hinder the development of other plants, are furnished by the Gout-weed (*Ægopodium Podagraria*), the Stinging Nettle (*Urtica dioica*), and the Fuller's Thistle (*Cirsium arvense*). Wherever these have settled on cultivated ground and penetrated the soil with their offshoots there is nothing for it but to dig up the whole ground and to carefully remove all the shoots. Unfortunately even this laborious task is not always rewarded with the desired result, for in spite of the utmost care it may happen that small fragments remain, and these form the nucleus of a new colony of weeds. In a short time a new group appears above the soil which has been cleared with so much care, and a fresh digging and still more careful clearing of the ground is necessary. These clustered colonies have a characteristic appearance when foliage-leaves spring from their underground stem-structures, the large blades being borne on almost equally long erect stalks, as is the case, for example, in the Butterbur (*Petasites officinalis*) and numerous tropical Aroids. Wide tracts are then to be seen covered exclusively with their large luxuriant foliage-leaves, all other vegetation being suppressed. The formation of offshoots and the production of clustered colonies also occurs to a remarkable extent in the common Reed (*Phragmites communis*). Once settled on suitable soil it will cover the widest areas in uninterrupted and unhindered march, suppressing and destroying all other plants. On the lower Danube there are many lowlands so thickly set with Reeds that in several hours' journey only a few small inconspicuous plants will be seen beside the Reed haulms. This Reed is also interesting from the fact that its offshoots can arise just as well under water as under the ground, and it may serve, in some respects, as the type of a group of plants which, by reason of their amphibious nature, play an important part in the transformation of submerged into dry land.

On the other hand, the variety of the protonemal threads, runners, shoots, and creeping stems which spread above-ground from the offshoots of these colonies is almost inexhaustible. And this is readily intelligible. The processes which are connected with their formation are much more varied in plant-members which grow

in the light and in open air than in those which develop under the water or the soil, or, perhaps we should rather say, that above the ground the greater fluctuations in light, moisture, and temperature bring about corresponding modifications in the vital processes. Moreover, the substratum presents every imaginable gradation from shifting quicksand to heavy clay, from steep rock-faces in one place to the bark of old tree-trunks in another, all these having by no means the same effect on the formation of offshoots. One of the most noteworthy processes occurring above the ground leading to the formation of clustered offshoots is that exhibited by Moss-protonemas. By protonema is meant a web of threads which spreads sometimes as a loose, open network, sometimes as a thick felt, over rock, clay, sand, earth, humus, bark, and decayed wood, the individual cells becoming the starting-points

Fig. 445.—A section through soil permeated by the protonemal threads of the Moss *Pottia intermedia*. (Magnified.)

of new Moss stems. This protonema may be compared to a web of Strawberry runners which has spread over the ground in a wood-clearing. Just as small plants spring up from the thread-like runners in this case, so Moss-plants are produced from the protonemal threads, and by the dying away of the latter become isolated. In many Mosses the end comes with the formation of this clustered arrangement, as, for example, in the tiny Mosses classed together as Pottiaceæ, of which one species, *Pottia intermedia*, is shown in fig. 445. This plant has the following remarkable history. During the period when most other plants are engaged in active nutrition and reproduction it remains with its rhizoids and part of the protonemal threads imbedded in the ground. Numerous scattered spores also remain resting in the ground until at length the time for aërial development arrives. Strangely enough, however, this is not until late in the autumn, when the leafy trees have discarded their foliage and autumnal mists drift through their bare branches. Then on the surface of the bare, cold, damp earth appear green threads which at first look like algal filaments, and on these small buds are formed (see fig. 445). In the course of a few weeks Moss-plants grow up from these buds

which become independent by the gradual withering and decomposition of the connecting pieces of thread. They form spherical spore-capsules, and with the scattering of the spores they wither and die. These plants are only a few millimetres high, but they are clustered together in such thousands that they form a velvety carpet over the soil, their emerald-green colour being the more striking as the last remains of the neighbouring vegetation have assumed the dull hues of decay. The Luminous Moss (*Schistostega osmundacea*) growing in the holes and clefts of slate mountains (already described in vol. i.), the protonema of which is depicted in Plate I., also forms loose colonies of separate Moss-plants from the green threads which creep over the clayey soil in the hollows. These plants die off after they have ripened their fruits. Of course the development is in this case not so rapid and does not occur in the late autumn as in *Pottia intermedia*.

A peculiar formation of offshoots may be noticed in epiphytes which climb over the bark of old trees and possess only short ribbon-like roots adhering to the damp bark, but none which grow down into the ground. Their stems and leaves invest the substratum like a carpet, as, for example, in several tropical Aroids of the genus *Pothos*, and in *Marcgravia*. The growing stem forks, and later on by the dying away of older portions behind the fork the two branches are separated and isolated. Each in its further growth may go a different way, one climbing up this and the other up that branch of the tree-trunk which serves as support; and, since this process is repeated, several independent plants of *Marcgravia* and *Pothos* may be found on the crown of the tree, all of which are to be regarded as natural offshoots. The same thing occurs in numerous Ferns, which grow on the bark of trees and in the humus-filled clefts of rocks, and in all those plants whose creeping aërial stems grow and branch at one end while they die off to a corresponding extent behind, as in many creeping species of clover, for example. As the annual increase in the stem of these plants is but small, the separated individuals move very slowly from one another, and several years elapse before the offshoots have formed a group which extends over an area of a square half-metre.

The result is obtained comparatively much quicker when the offshoots are formed by runners and shoots. In one section of these plants, of which the *Saxifraga flagellaris* (fig. 446), a plant widely spread through the Arctic region and in the high mountain districts of the Himalayas, Altai, and Caucasus, may be taken as a type, only a single bud is developed at the end of a slender thread-like shoot. This takes root where it touches the ground, and grows up into a rosette. Not until the nourishment of the rosette by the rootlets which have been sent into the ground is assured does the long thread, terminated by the bud, die off, the connection with the mother-plant being thus severed, whilst the rosette now forms an independent plant. Since the shoots are usually numerous and radiate outwards the mother-plant in course of time becomes surrounded with an actual garland of rosette-shaped offshoots, and in a few years a fairly large area is covered with hundreds of larger and smaller rosettes, which, however, no longer show the circular arrangement, because the shoots of neighbouring rosettes often cross, and consequently the circles intersect.

Everyone knows the long runners of the Strawberry plant (*Fragaria vesca*). Here buds arise at the intermediate nodes as well as at the tip of the runner, and these develop into new plants after the thread-like connecting portions have perished. Suppose a Strawberry stock sends out three runners during the summer; each takes root at 5 nodes, and from each node a bud, *i.e.* an offshoot, develops, so that the following year the mother-stock is surrounded by fifteen daughter-plants. It should be noted that the length of the internodes in each runner is unequal. For example,

Fig. 446.—Formation of a clustered colony by means of aerial runners in *Saxifraga flagellaris*.

in one which had extended over the ground in the shade of the wood, the first internode was 37, the second 34, the third 31, the fourth 30, and the fifth and last 22 cm.; thus the offshoots were the closer together the greater their distance from the mother-plant. Next summer fifteen new offshoots were again formed from each of the original fifteen, arranged in exactly the same way, and in the forest-glade, where two years previously there had been only a single Strawberry plant occupying a space of 50 sq. cm., there would now be 200 plants distributed over a space of about 3600 sq. cm.

The lesser Spearwort (*Ranunculus reptans*), the Ground Ivy (*Glechoma hederacea*), and the creeping Cinquefoil (*Potentilla reptans*) display quite as

considerable an increase and distribution as Strawberries. The accompanying table gives the length of runners and shoots of some well-known species in which the formation and rapid distribution of offshoots is particularly noticeable on suitable substrata.

	Centimetres.		Centimetres.		Centimetres.
Saxifraga Aizoon	4	*Lycopodium annotinum*	30–40	*Vinca herbacea*	70
„ *cuneifolia*	6	*Saxifraga sarmentosa*	40	*Fragaria Indica*	85
„ *Geum*	8	*Ranunculus Flammula*	50	*Potentilla anserina*	110
„ *flagellaris*	10	*Geum reptans*	50	*Glechoma hederacea*	126
Sempervivum stenopetalum	12	*Glyceria fluitans*	50	*Potentilla reptans*	130
Viola odorata	13	*Lithospermum purpureo-cæruleum*	56	*Rubus saxatilis*	140
Arabis procurrens	16	*Ranunculus reptans*	60	*Fragaria vesca*	150
Androsace sarmentosa	18	*Tiarella cordifolia*	65	*Vinca major*	200
Ajuga reptans	20	*Vinca Libanotica*	66	*Rubus Radula*	300
Hieracium flagellare	30			„ *bifrons*	650

In those cases in which plants change their position by the development of offshoots in any direction, whilst they die off in the opposite one, progress is always restricted. The offshoots penetrate only by slow degrees in the surrounding soil, and many years elapse before a space of 100 metres is traversed in this way. The change of position is much more rapid when the offshoots become detached from their place of origin and are carried to a new spot by special mechanisms of transit, by currents of water, the wind, or finally by the help of men or animals. In this way it may happen that single detached cells, cell-groups, buds, and shoots may be carried vastly further than 100 metres in a few minutes, through long valleys, over steep precipices, or even over high mountain ridges. This rapid distribution is not indeed so certain in its result as the slower mode of progression. It may easily happen that the wind or water current lands the detached offshoot on some spot where further development is impossible, where it must inevitably perish. Apparently, however, this disadvantage is compensated for by the immense quantity of such detached offshoots. Again, there are plants which form two kinds of offshoots, those which propagate slowly but surely, which are few in number, and others, developed in large numbers, which are distributed rapidly but less certainly.

Only a very small proportion of plants develop offshoots which after they become detached reach a new locality spontaneously, by means of special organs of motility. This class of brood-body is always aquatic and of very small size, and its development can only be followed under the microscope. The best-known examples are Fungi, belonging to the Saprolegniaceæ and Chytridiaceæ, the dark green Vaucherias, and other species of Algæ. The Saprolegnias are saprophytes growing in and on the bodies of animals which have died in the water—not only fish, crustaceans, and insect larvæ, but also birds. They form delicate, thread-like, tubular hyphæ, which ramify repeatedly, and part of which penetrate into the corpse like a root-plexus, while the rest rise up above the body in the form of white or grey felt, which floats in the water. Single tubular erect hyphæ assume a knob or club-shaped form, and their protoplasm divides up into numerous portions. Ultimately the club-shaped tube opens at the apex, and the little proto-

plasmic bodies (swarmspores) escape (*cf.* fig. 192, p. 17). What happens next differs according to the species. In the genus *Saprolegnia* the individual swarmspores have two cilia, by means of which they immediately swim away (see figs. 192[6] and 192[7]); in *Achlya*, on the other hand, the swarmspores group themselves into a round ball in front of the opening of the tube as they escape (*cf.* fig. 192[1, 2, 3, 4]), and at first possess no cilia. They surround themselves there with a delicate capsule, which apparently consists of cellulose, but they do not remain long in this condition. A few hours after, they leave the capsule and assume a bean-shaped form, being now provided with cilia which enable them to swim about in the water. They only swim about for a comparatively short time. When they have settled on some spot they lose their cilia, surround themselves with a cell-wall, and become the starting-point of a new plant; therefore they must certainly be regarded as offshoots. The Chytridiaceæ have a similar offshoot formation. These too are devoid of chlorophyll, but they are true parasites, not saprophytes like the Saprolegniaceæ. They prefer green water-plants for their hosts, penetrating into their cells, killing and destroying the protoplasm, and then develop thick tubes which project beyond the host-plant, and in which the protoplasm becomes divided up into numerous spherical portions. The tubes open at their apex sometimes by the raising of an actual lid (see fig. 192[5]), sometimes by the dissolution of a limited portion of the cell-wall, so that a hole results from which the isolated protoplasts are expelled. On its escape each of these offshoots is spherical or egg-shaped in form, and possesses a single long cilium. This cilium serves as a swimming organ which in many species actually causes a hopping and springing movement. In order to avoid repetition, we may refer to the description of the swarmspore-formation given at vol. i. p. 29, in the case of the Vaucherias and Sphærellas.

On the whole, as we have already stated, the formation of offshoots which swim about independently in the water and seek out new spots suitable for settlement is restricted to a very small section of water-plants. Offshoots which, after their detachment from their place of origin, are carried passively by water currents without exercising any directive influence, and are stranded at some distant spot, are of much more frequent occurrence. Of these water-plants we might mention in the first place the filamentous green Algæ which cover with slimy masses the surface of slowly moving water or stones at the bottom of rapid streams. In many of these plants several times during the year do the dividing membranes between the individual cells break down into mucilage so that the cells become free and are carried away by the flowing water. Each of these cells may again give rise to a new thread by repeated division. We cannot easily conceive a more simple method of propagation and distribution than this. The offshoot-formation in the Florideæ is hardly less simple. Whether the whole plant is composed of rows or of open networks of cells, four protoplasmic balls, the so-called tetraspores, are formed in various situations on the plant; these are liberated into the surrounding water and carried away by the current. They adhere to some firm spot under water and there grow up into new plants. In most instances the protoplasm of the cell in

which the offshoot formation occurs is divided into four, more rarely two or eight clumps are formed by the splitting and dividing of the protoplasm, and most rarely of all is the whole undivided protoplasm of a cell transformed into a single offshoot.

The small group of water-plants known as the Hydrodictyaceæ display a peculiar offshoot-formation. In the elegant Water-net (*Hydrodictyon utriculatum*, *cf.* p. 640), whose cylindrical cells form a closed net with hexagonal meshes, the cells each originate new plants as Water-nets in miniature. The protoplasm in one of

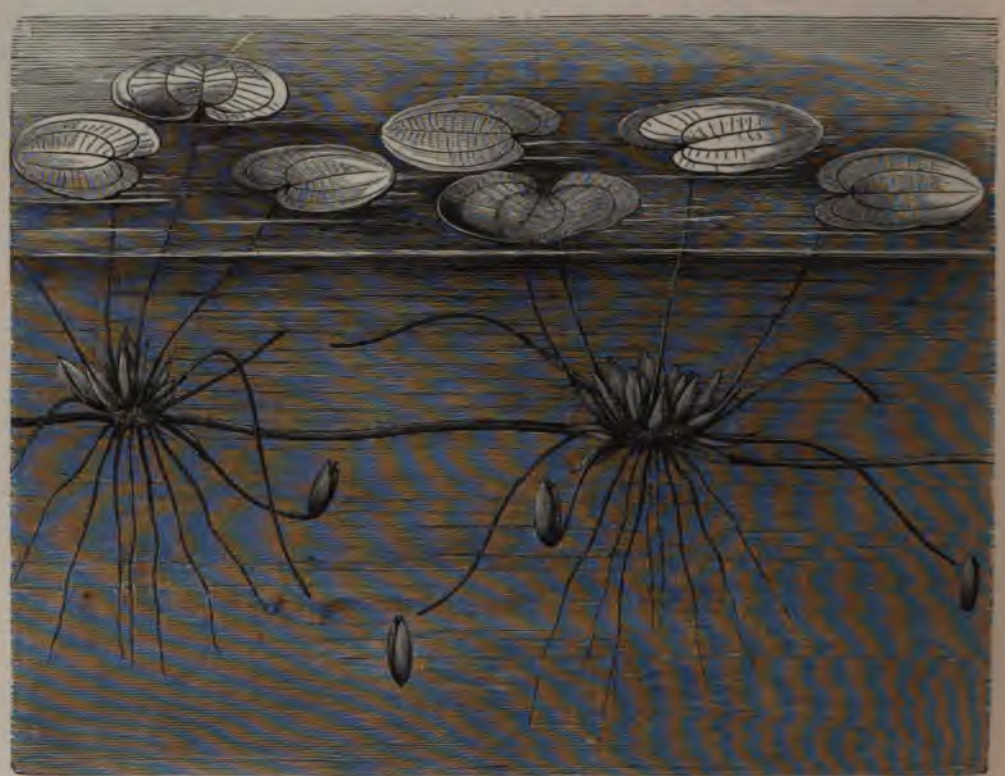


Fig. 447.—Frogbit (*Hydrocharis Morsus-ranæ*). The winter buds in process of detachment from the ends of the submerged stolons.

the cells which is preparing for offshoot-formation divides into many thousand parts which quiver in a remarkable way and pass between one another, and are said to undergo the so-called swarming motion. This lasts about half an hour, then the swarming portions, whose rod-like form can be recognized in spite of their minuteness, come to rest, arrange themselves into nets with hexagonal meshes (see figs. 370 [3, 4, 5], p. 640), and now each cell contains a tiny Water-net. The outer layer of the cell-wall in which this grouping has taken place is partially dissolved. The little net, at first still inclosed in a pellicle of protoplasm, slips out and swims freely in the water as an offshoot. In 3–4 weeks it has attained the size of the Water-net, from one of whose cells it emerged, and in each of its own cylindrical cells the same process may be repeated. A similar process is observed in the small water-plant

called *Pediastrum*, which is closely related to the Water-net, and of which one species is shown in figs. 370[6,7,8], p. 640.

The distribution of bud or sprout-like offshoots is seen especially in the Duckweeds, Alismaceæ, Potamogetons, Utriculariaceæ, Droseraceæ, and Primulaceæ. Most of the Duckweeds (e.g. *Lemna polyrrhiza* and *L. arrhiza*), which float during the summer on the surface of still water, towards the autumn form organs on their flattened stems which become detached from the summer plants, sink to the bottom

Fig. 448.—Frogbit (*Hydrocharis Morsus-ranæ*). [1] Winter buds rising to the surface in spring. [2] Young floating plants which have developed from such buds. [3] Older floating plants.

of the lake, and stay there during the winter. Each of these organs is pocket-shaped, and in the hollow the next year's shoot is already laid down—of course, as a minute structure whose semicircular free end scarcely projects above the closely-adjoining edges of the pocket. These detached winter buds sink because their cells, even those of the epidermis, develop large starch grains which are crowded together, and literally fill up the lumens of the cells. There are no air-spaces like those which cause the summer-plants to float on the surface of the water; the stomata as yet are closed, and the whole body, hermetically sealed from the outer world, now has a specific gravity which causes it to sink down to the bottom of the water, where it is protected against the frost. There it remains in a resting condition during the winter. At the beginning of the warmer season the bud wakes from its winter

sleep, the starch-grains are used up in the building of the young stem, and the growing buds of these species of *Lemna* again rise to the surface of the water, because the cells which had served as storehouses for the starch become empty, and because air-spaces are formed in the new tissues.

The same change of position during the year is also observed in the offshoots of the Frogbit (*Hydrocharis Morsus-ranæ*), which is common in still waters through the whole of Europe and a great part of Asia. Although this plant is abundantly provided with roots, it never fixes itself by them to the slimy bottom of the pool in which it lives. Throughout the summer it remains floating on the surface, spreading its foliage like the Water-lilies on the top, while its roots hang below in the upper layers of water. Its propagation in the summer is very rapid by the formation of offshoots. These arise in the axils of foliage-leaves from the very short, erect, floating stem, and are rather long, resembling thick threads, which keep close to the surface of the water, and grow in a horizontal direction. Each shoot terminates in a bud, and this quickly opens, sending up green foliage to float on the water, and a bunch of roots below. In a very short time the plant thus formed resembles the parent which gave it origin, and is itself able to develop new shoots. Thus it comes about that in a few weeks the surface of the water is covered with innumerable floating plants of Frogbit, every 10–20 being connected together by horizontal strands. The pretty flowers now rise above the surface from the stronger plants. The flowering is, however, of short duration, and is seldom successful, *i.e.* fruits with fertile seeds are rarely produced. As soon as the blossoming is over and autumn approaches, new shoots ending in buds appear. They are shorter than those of the spring, and they sink lower on account of the greater weight of the buds they carry. The buds, too, have a rather different form. They are firm, and wrapped in closely-fitting scale-leaves, and they almost attain the size of a small date-seed. As soon as the bud is provided with the requisite amount of starch and other reserve food-substances, it becomes detached from its filamentous support, and sinks down (see fig. 447) till it rests on the mud at the bottom of the pond. The plants floating above, which gave rise to them, die off completely and decay. It is high time indeed to quit the field above, for the surface of the water is soon covered with a sheet of ice, which renders all vital activity impossible for months. When spring again arrives, and the ice vanishes from the pools and ponds, new life rises up from the mud below. The buds of the Frogbit which have passed the winter there become spongy, the cell-cavities fill with air, and the whole structure rises to the surface (see fig. 448[1]). Arrived there the scale-leaves rapidly separate, green leaves expand their blades on the sunlit surface, roots hang down into the water, and before long, shoots are again developed as already described (fig. 448[2]). Obviously deviations of position and sometimes considerable changes of place are brought about by the sinking and rising of the buds in the water. It is observed, too, that the Frogbit is very variable in regard to its position, and that sometimes a place whose surface was one year covered with numberless plants will in the year following present no trace of them, while new colonies will have developed at a distance.

The Bladderworts (*Utricularia*), Aldrovandias (*Aldrovandia vesiculosa*, see vol. i. p. 151), and the Water Violet (*Hottonia palustris*), which desert the cold upper strata of water as winter sets in, and sink down to the relatively warm depths below, develop special wandering buds for this purpose; these are not enveloped in scale-leaves like those of the Frogbit; they are in reality merely much abbreviated shoots whose leaves are so crowded and folded so closely together, that the whole shoot looks like a rounded green ball. These balls at first remain connected to the piece of the floating stem which gave them origin. This attachment is lost towards the end of autumn, and the little buds sink down to the bottom of the pond and necessarily get distributed in various directions. Next summer, when the balls leave their winter quarters and are again carried to the upper strata of water, they expand into foliage-bearing plants. It has been already stated (vol. i. pp. 76 and 658) that the Water Soldier (*Stratiotes aloides*), which is closely-related to the Frogbit, undergoes similar changes during the year, and we need here only draw attention to the fact that it sinks down to its winter quarters at the bottom of the pond as an open rosette, and not in the form of buds, and rises again the ensuing spring when the weather is more favourable.

The Pondweeds *Potamogeton crispus, obtusifolius, pusillus*, and *trichoides* behave differently from the marsh and water plants hitherto described. Here, as autumn approaches, buds are developed which become detached from the old decaying stems (fig. 136, vol i. p. 551), and sink down to the bottom of the pond; but in the following summer they remain sticking in the mud at the spot where they fell, and do not rise again to the surface. They send out roots and develop much-branched leafy stalks, and these rapidly grow up to the surface of the water. These Pondweeds, firmly rooted to the bottom of the pond, multiply not only by these free-swimming offshoots, but also by stolons which creep far and wide through the mud; but of course the plants are distributed to much greater distances by the sprouts or buds which are developed in the autumn on the upper internodes, and which then become detached and float in the water, than would be possible by the creeping stolons alone.

A very remarkable distribution of offshoots is to be observed in the marine *Cymodocea Antarctica*, which is very common on the coast of Australia, south of the Tropics. This plant has an erect stem, thickly covered with dull-green foliage-leaves, arranged in two rows. The lower leaves fall off prematurely, and the bare scarred stem then carries only a bunch of ribbon-shaped leaves at its summit. Towards the close of the winter the end of the stem above these leaves is seen to become peculiarly modified. Its internodes become much contracted, and at the lowest node is developed a scale-leaf with four lobes, which surrounds the leaves developed from the upper nodes, like a cup. Buds arise in the axils of one or two of these leaves, while the leaves themselves die and decay. The parenchyma of the four-lobed, cup-shaped scale-leaf also decays, and only its stiff veins remain, so that instead of the cup, there are now only comb-like scales. After this alteration has taken place, the tissue of the stem below the pectinate scales breaks across,

and the whole shoot-apex, separated from the lower part of the stem, which has long been in a leafless condition, is carried away by the currents of the water. How far and for how long the shoot is carried about depends upon the local condition of the sea-shore. Sooner or later its career of wanderer is arrested by the trailing comb-like scales assuming the rôle of anchors. As soon as the anchor is fast, some 2–4 roots develop from the lower internodes of the shoot; these pass between the teeth of the comb-like anchor, and grow down into the muddy substratum, thus fixing the offshoot. All this happens at the end of winter. During the following summer, the shoot, which is about 8 cm. long, and is anchored and rooted in the mud, again grows up into a stem about a metre high, and next winter its top again falls off just in the same way. It has already been mentioned (p. 457) that this strange sea-plant very rarely blossoms or fructifies—a circumstance which confirms the supposition that the boundless colonies of it round the coasts of Tasmania owe their origin to the offshoots distributed by the sea currents.

The distribution of offshots by sea-water is a much simpler affair in the Sea-wracks, Ulvas, and Florideæ than in these other water-plants. When the sea is stirred to its depths by violent storms and the spring-tide is higher than usual the retreating waves leave any quantity of fragments of these plants behind them. These have been torn by the raging water from the firmly-fastened ribbons, nets, and threads below, and are then carried away by the billows. The water drives them into clefts of the rocky coast or imbeds them in the sand and mud of the shore, and, wonderful to relate, not a few of them flourish again, granted of course that they are not speedily removed by subsequent tides and that the circumstances are otherwise favourable.

Much the same kind of thing happens on the banks of rivers and streams. A portion of the plant-fragments brought by floods and stranded on the mud of calm inlets undergoes decomposition. A larger portion remains fresh and living, sending out roots and vigorous shoots. In the bed of the Danube, in addition to the abundant creeping shoots of the Reeds (*Phragmites*) and various Sedges, Bulrushes (*Scirpus, Typha*), broken twigs of *Salix fragilis*, bits of roots of the Sea Buckthorn (*Hippophae rhamnoides*), fragments of the rhizomes of *Œnanthe Phellandrium* and *Acorus Calamus*, leafy twigs and stolons of various species of Pondweed, Water-Milfoil, and Water Ranunculus (*Potamogeton, Myriophyllum, Ranunculus aquatilis*) are all distributed in this way. Sometimes these growths settle in places where formerly no specimen of the kind had been seen for miles, and the fact may be easily confirmed that the distribution of their offshoots is actually brought about by flowing water in a very short time to great distances and in great abundance.

The distribution of offshoots in little brooks which flow down between Reeds and Rushes with a moderate fall, and scarcely ever overflow their banks takes place more quietly. A rapid flow occurs only in the middle of the channel, but near the bank, and especially in the small inlets, the water is almost as still and calm as in a closed-in lake. Here in these quiet spots are also to be found floating

plants brought by birds; their roots are either not fixed to the ground but sway about in the water, or they may be altogether absent; examples are, *Riccia fluitans* and *R. natans*, *Lemna* and *Wolffia*, and in tropical regions *Azolla* and *Pistia*. All these multiply very rapidly. While they continually branch at one end, forming spreading lobes and sprouts, they die away on the other, the result being of course a separation into several pieces, *i.e.* into offshoots. These fragments spread themselves like a green mosaic over the surface of the water. As the offshoots increase in numbers a certain number of them will extend beyond the calm inlet by the bank into the flowing water in mid-stream. Here they are hurried away by the current, and it often happens that they travel some distance before they are again stranded in some calm spot near the bank to form again the starting-point of a fresh aggregate of offshoots.

Rain-water also plays an important part in the distribution of offshoots. Those of the widely spread Liverwort, *Marchantia polymorpha*, so frequently met with on damp earth, are especially noticeable in this respect. Their development is represented in fig. 196, p. 23. On the surface of the dark-green leaf-like thallus of this Liverwort cups arise, at the base of which papillae give origin to plate-like brood-bodies (gemmæ, *cf.* figs. 196[2] and 196[3]). Other papillæ behave differently, and undergo only slight enlargement. The heads of these latter then swell up forming a gelatinous mass, and as this swells up it raises the green gemmæ higher and higher out of the bottom of the cup (fig. 196[2]). At last they get close to the edge and are washed out of it by the rain. The offshoots of other Liverworts are also chiefly distributed by rain-water, as for instance the gemmæ which arise in the crescent-shaped pockets of *Lunularia*, and in the flask-shaped cavities of *Blasia pusilla*. The pairs of cells which arise on the upper surface of *Aneura multifida*, the single cells which become detached from the edge of the fronds of so many Liverworts, the multicellular offshoots which are given off by *Radula complanata* so common on the bark of trees, the round cell-plates growing on the edge of the leaf-like thallus of *Metzgeria pubescens*, and finally the ball- and disc-shaped groups of cells which develop on the surface of the leaves of numerous Mosses (*e.g.* on various species of the genera *Leucobryum*, *Grimmia*, *Zygodon*, *Orthotrichum*, *Barbula*, *Calymperes*). In many of these cases the small offshoots are detached as well as distributed by the action of rain-water, but in others the loosening occurs before the rain begins, and in *Blasia* and *Aneura*, as well as in *Marchantia*, the offshoots are first separated by mucilaginous membranes, and are thus raised up from their attachment. Not until afterwards are they washed out and distributed by the falling rain. These small offshoots can of course also be carried away from their place of origin by strong gusts of wind. Even breathing strongly on them is sufficient to detach the uppermost gemmæ of *Marchantia*, but in dry air and in dry soil they rapidly shrivel up and perish. The distribution by currents of air is therefore not attended by success, but the offshoots of the Liverworts and Mosses washed out by showers of rain immediately begin to grow, and quickly attain to further development. This mode of distribution plays an

important part in the covering of tree-trunks with Mosses and Liverworts. A small patch of *Radula*, *Metzgeria* or similar plant having once taken hold, when a downpour of rain beats upon the trunk quantities of tiny ball- and disc-like offshoots float away to be caught again by projecting irregularities of the surface; indeed the rapid covering of old trunks with green carpets and mantles of Liverworts and Mosses is for the most part effected by rain-water.

It is comparatively seldom that bud- and sprout-shaped offshoots are distributed by rain. But there is one very interesting example of this, viz. the widely-spread Lesser Celandine (*Ranunculus Ficaria*), a single plant of which is shown in fig. 343 [3], p. 460. In the axils of the foliage-leaves of this plant are developed offshoots which have the form of small tubers, and which are not unlike the youngest stages of small potato-tubers (fig. 343 [6]). When the leaves and stalk of the Lesser Celandine begin to turn yellow and wither in the early summer, the tubers break away from the stem and fall to the ground. There they usually escape observation, since they are hidden by the yellowing foliage; but should there come a heavy storm of rain the withered leaves are pressed down on to the soil by the force of the rain-drops, and the scattered tubers become visible. Sometimes the impact of the falling rain-drops hastens the detachment of the tubers from the mother-plant. When the rain is so heavy that the water flows away in the form of small rivulets, the loose tubers are washed off in abundance. A sudden downpour of rain in a region abundantly overgrown with Lesser Celandine is sufficient to float away numbers of the tubers, and heap them up on the borders of irrigation channels when the rain disperses. In such places the quantity of tubers which have floated together is often so large that one can hardly gather them in one's hands. In this way arose the idea that the tubers had fallen from heaven with the rain, and the myth of a rain of potatoes.

The small tubers which arise in the axils of the leaves of *Gagea bulbifera* (*cf.* fig. 343 [1], p. 460), a plant growing on the steppes of Southern Russia, are distributed by rain-water just like those of the Lesser Celandine. This brings us to the question of the much-discussed manna-rain in steppes and deserts, which in reality is nothing but the distribution of the offshoots of a Lichen, viz. the Manna-lichen. This Lichen, which was termed *Lichen esculentus* by the older Botanists, but in recent times has been referred to the genera *Urceolaria*, *Lecanora*, *Chlorangium*, and *Sphærothallia*, and which apparently consists of three species, viz. *Lecanora esculenta*, *L. desertorum*, and *L. Jussufii*, is spread over an enormous region in south-west Asia, and extends as far as the south-east of Europe and the north of Africa. This Lichen is met with in the neighbourhood of Constantinople, in the Crimea and Caucasus, in Persia (whence the illustration at page 695), also in Kurdistan, Arabia, and the Anatolian high land from Bulgar Dagh in the Taurus (where it is very often met with at a height of 2700 metres above the sea), and finally in the Sahara and the deserts of Algeria. It first forms thick wrinkled and warted crusts on the stones, preferably on small fragments of limestone lying about; the outer colour of the crust is a grayish yellow, while on breaking it appears as

white as a crushed grain of corn. As they get older the crusts become rent, and separate either partially or wholly from their substratum. When they first become loosened the edges of the detached portion become somewhat rolled back. The rolling then continues, and ultimately the loosened piece forms an elliptical or spherical warted body with a very much contracted central cavity. Small stones are sometimes imprisoned in this way within the cavity of the sphere, in which case the weight of the loose Lichen is correspondingly increased, but as a rule the hole is filled with air, and when dried the pieces weigh very little. Ten loose pieces of Manna-lichen, each as large as a hazel-nut, weighed 3·36 grams, and the weight of a single piece therefore was on an average only ·34 grams. It is easy to see that the loose portions will be rolled about by the wind, and that a storm will sometimes sweep them up from the ground and carry them hither and thither through the air. This method of distribution appears to be the prevailing one in regions where the supply of water is not abundant in the rainy season, and where violent storms rage from time to time. That this is so is confirmed by the circumstance that the Manna-lichen after the storms lies chiefly piled up behind the low bushes and undergrowth, *i.e.* just where the force of the storm has been to some extent broken, and where the shifting sand has been heaped up into little hillocks. Where a period of heavy rains succeeds the long dry summer, however, and where such a quantity of water falls on the parched land that it cannot all be absorbed, some of the rain collects into small rivulets. These carry away with them everything which is movable and capable of floating. The turbid rivulets flow down over the inclined soil to the lowest parts of the country and there unite into larger streams, or if it can find no outlet the water remains for some time in the hollows as small pools and puddles, and deposits there the mud and vegetable débris it has carried with it. The latter is more especially the case on the steppe soil overstrewn with small stones where between the slight elevations there is a labyrinth of shallow channels and winding depressions resembling ploughed land. In such regions the Manna-lichen is chiefly washed into the depressions by the rain-water, and in some years in such quantity that they form heaps a span high, and a single man can in a day collect 4–6 kilograms (about 12,000–20,000 pieces, varying in size from a pea to a hazel-nut). This is especially the case in the steppe region and in the high lands of South-west Asia, where the Manna-lichen is used as a substitute for corn in years of famine—being ground in the same way and baked into a species of bread. That the rain-water is the agent which transports the Lichen in these regions is beyond doubt, because the pieces heaped up in the hollows are not in the least rubbed on their outer surfaces as would certainly be the case if they had been rolled and dragged even for only a short distance over stony ground. It is also remarkable that all the great so-called rains of manna, of which news has come from the East to Europe, especially those of the years 1824, 1828, 1841, 1846, 1863, and 1864, occurred at the beginning of the year between January and March, *i.e.* at the time of the heaviest rains. When we remember that the inhabitants of the district actually thought that the manna had fallen from heaven, and quite overlooked the

fact that this vegetable structure grew and developed (although only in isolated patches and principally as crusts on stones) in the immediate neighbourhood of the spots where they collected it, we need not be surprised at the conclusion of our own peasants who thought the tubers of the Lesser Celandine had fallen with the rain from heaven. It should be mentioned that the manna sent to the Israelites on their journey out of Egypt to the Holy Land is identical with the Lichen described here and figured on page 695, and the older view that the manna of the desert was the sap of a Tamarisk (*Tamarix gallica mannifera*) exuded under the influence of a parasite is without any foundation.

Spores take the first place among the reproductive bodies which are distributed by wind. Many Ascomycetes develop some of their spores by abstriction from the free ends of special hyphæ. These rise up into the air from the substratum, which is permeated or covered by the mycelium. In this way the separated but loosely-adhering spores can be carried away by the slightest atmospheric movement. In the Moulds known as *Aspergillus* and *Penicillium*, whole series of spores are cut off from the end of each hypha (see figs. 193 [4, 5, 8, 9], p. 18), and as they are crowded closely together a single breeze carries off innumerable quantities of spores. By breathing only lightly on the small forest-like colonies of supports the spores are whirled as dust into the air, and as they are extremely light they not only remain a long time suspended in it, but even in perfectly still air are carried sometimes up, sometimes down, by the currents due to slight differences of temperature, again being carried horizontally or whirled along until at last they settle, and become the starting-point of a new Mould formation. The spores abstricted from the ends of the so-called sterigmata in the Hymenomycetes (see figs. 389 and 390 [7]) may also be detached and carried away by wind, but apparently most of the spores in these Fungi separate spontaneously in calm air and fall to the ground, covering it with a delicate layer of dust, to be afterwards carried away from this resting-place by breezes.

The spores of Ustilagineæ and those in the æcidia of Uredineæ (see p. 686) are at first covered with delicate membranes and sometimes inclosed in special receptacles. As soon as they are mature they form a powdery mass, which bursts through the covering membrane, and the now exposed spores are blown away as dust by the wind. If they have developed in deep receptacles shaking is necessary before they can be blown away. The spores then fall from the mouth of the receptacle into the currents of air. In many Myxomycetes and Gasteromycetes (see fig. 367 [2], p. 618, and fig. 391 [3], p. 690) delicate twisted threads called the capillitium are developed simultaneously with the spores. The web of threads with the spores between them is inclosed in a membrane (see fig. 449 [1]). When this membrane bursts at maturity and the receptacle is thrown open only the spores in the immediate neighbourhood of the opening can be blown away by the wind, the deeper ones being held back by the capillitium. The lower layers of the capillitium are then raised by the action of dry winds, and thus quantities of new spores are continually carried from below up to the opening. In this way it happens that the spores of these plants are only

distributed in small detachments, and only at a suitable time, *i.e.* when a dry wind is blowing. A similar contrivance is exhibited by the Muscineæ in the Marchantiaceæ, Anthocerotaceæ, and Jungermanniaceæ. Peculiar filamentous, very hygroscopic cells with spiral bands of thickening on the cell-wall, are found with the spores in the receptacles of these plants (see p. 696). These have been called elaters, because it was thought that their movements caused the ejection of the spores. Their significance, however, rather lies in the fact that they serve to hold the spores together after the opening of the receptacle, and only expose them by degrees to the wind. They also help to burst open the receptacles, but that hardly concerns us just now.

Only three of the most striking of the varied contrivances for spore distribution by wind in Mosses (which are destitute of elaters) will be here described. First, those which are observed in the Andreæaceæ (see figs. 450 [1] and 450 [2]). Here the capsule opens by four longitudinal clefts which, however, do not extend quite to the free end, and the four pieces into which the wall is thus divided may be compared to the staves of a barrel joined together at the top. In damp weather they become approximated, so that the clefts are closed (fig. 450 [1]). In dry weather the valves become arched, the clefts widen, and the spores may be blown out from the interior of the capsule by the dry wind (fig. 450 [2]). The distribution of the spores is effected quite differently in the Polytrichums, one species of which is illustrated in figs. 450 [3, 4, 5, 6, 7, 8]. After the roof (operculum) which formerly surmounted the capsule has fallen off a delicate whitish membrane comes into view, which is held fast by the points of numerous sharp teeth, and is stretched like the skin of a drum over the mouth of the capsule with its annulus. If rain and dew moisten the Moss the teeth are seen to be much bent inwards, the membrane lying upon the annulus, and completely closing the receptacle (fig. 450 [5] and 450 [7]). But in dry air, especially when a dry wind is blowing, the teeth turn rather outwards, raising the membrane above the annulus, and thus small holes are left between the teeth through which the spores can escape (figs. 450 [6] and 450 [8]). The same dry wind which causes the alteration in the position of the teeth now shakes the spores out of the capsule, which is borne on an elastic seta. *Grimmia ovata*, one of the Bryaceæ (see figs. 450 [9] and 450 [10]), may be taken as the type of a third contrivance for exposing the matured spores to the wind in dry weather, retaining them in the receptacle when it is damp and protecting them there from the injurious effects of moisture. The circular mouth of the pipe-bowl-shaped receptacle is furnished with

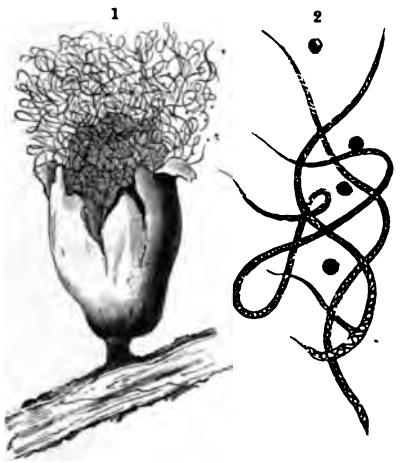


Fig. 449.—*Trichia clavata*.

[1] The membrane of the sporangium has burst, and the capillitium has bulged out raising up the spores embedded between its threads and exposing them to the wind; ×20. [2] Threads of the capillitium with the spores lying between them; ×250.

teeth, each of which terminates in a free point. The tissue of these teeth is hygroscopic, and their direction and position alter to a surprising extent according to the degree of humidity of the air. In damp weather the teeth are so close together that they completely shut the capsule (fig. 450[9]), but in dry weather they bend outwards (fig. 450[10]), and the spores are shaken out of the capsule and scattered by the wind.

We shall have to describe presently how the sporangia of most Ferns dehisce

Fig. 450.—Dispersal of spores by wind.

[1] Spore-capsule of an *Andreæa* in damp weather. [2] The same in dry weather. [3] Spore-capsule of a *Polytrichum* in damp weather. [4] In dry weather. [5] The spore-capsule of a *Polytrichum*, the edge of the mouth beset with teeth and covered with a membrane, in damp weather. [6] In dry weather. [7] A part of the peristome more highly magnified, in damp weather. [8] In dry weather. [9] Spore-capsule of a *Grimmia* in damp weather. [10] In dry weather. [11] Racemose sporangia of a *Botrychium* in damp weather. [12] In dry weather. [13] A single sporangium of this *Botrychium* enlarged, side and front view, in damp weather. [14] In dry weather. [1], [4], [11] and [12] nat. size; the others enlarged.

suddenly so as to scatter the spores. In such Ferns the sporangia are developed on the under side of the frond, and this position protects them excellently against any injury which might befall them from rain or dew. But there are some Ferns whose sporangia are exposed to both rain and dew, and whose spores are not suddenly scattered by the bursting of the sporangia. Among others, the Moonwort (*Botrychium*) may be mentioned. Its branched spike of sporangia is represented in figs 450[11] and 450[12]. The elliptical sporangia of the Moonwort open by a transverse slit, but the two valves thus formed only separate in dry weather (figs. 450[13]

and 450[14]) when the spores may be shaken out and blown away. As soon as the sporangia are moistened the two valves immediately shut together (figs. 450[11] and 450[13]) and obviously the spores can no longer be shaken out. A similar opening and shutting of sporangia according to dryness or moisture may also be observed in the Lycopodiaceae (see fig. 405[4], p. 716).

A similar phenomenon may also be observed in the sporangia of the Horse-tails (see fig. 403[4], p. 712). Here not only the sporangia but the spores themselves present a very different appearance according as they are dry or damp. The wall of these spores consists of several layers, of which the outermost splits up spirally to form two arms which remain joined to the spore at one spot. In dry weather the two spiral bands, which are arranged in the form of a cross, unroll (see fig. 451[1]) and constitute four appendages which afford enough purchase to the wind to enable the comparatively large and heavy spores to be carried away. If the spores fall on to

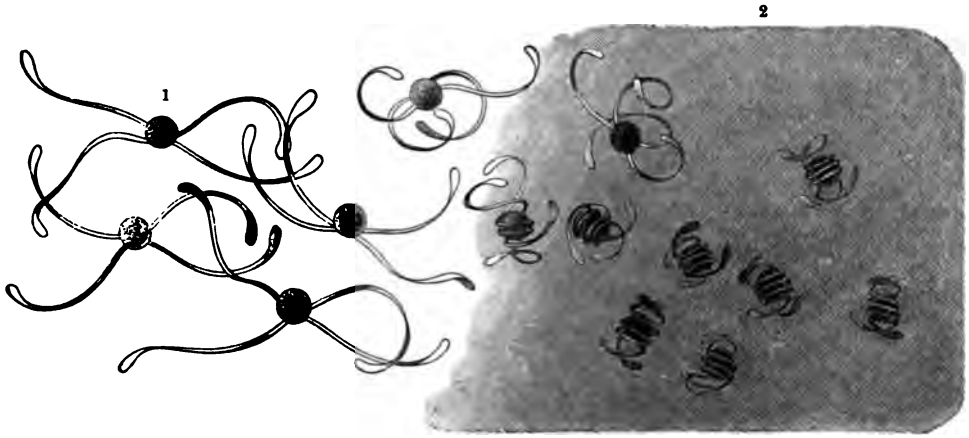


Fig. 451.—Spores of the Horse-tail *Equisetum Telmateja*.

[1] In dry; [2] in moist condition; ×25.

some spot of earth which, on account of its dryness, is not suitable for their germination the wings remain widely outspread. The next gust of wind raises them up again and carries them to another place. If, however, the resting-place is moist, and if the conditions are favourable to the growth of the *Equisetum*, the bands roll up spirally (see fig. 451[2]). In this way the spores may become fastened to a projecting object, and if this should not be the case at least the rolling up of the bands produces a diminution in size, and the spores are not easily again blown away from a suitable damp resting-place. Another explanation as to the function of these structures has also been offered, namely, that by means of the repeated expansions and contractions of these hygroscopic arms the spores are linked together as it were arm in arm. Further reference to this will be found at p. 713.

The soredia of Lichens must also be mentioned as asexual reproductive bodies which are distributed in enormous quantities by currents of air. To the naked eye they look like a floury dust deposited in places on the Lichen thallus. These dusty masses are built up of green cells, either solitary or in groups, which are wrapped

round by colourless hyphal threads. They arise in the interior of the Lichen body, and are ultimately pushed out on the surface by the rupture of the pustules in which they arise. The wind raises and carries them away, and if they happen to fall into the cleft of a rock or into the crevices on the bark of a tree they immediately grow up into a new Lichen body which agrees in every particular with the parent plant and is itself able to again produce soredia. The genera *Stereocaulon*, *Evernia*, and *Pertusaria* are especially noted for their abundant formation of soredia. The shrub-like, branched *Stereocaulon coralloides* is often so thickly covered with soredia that the whole Lichen looks as if it had been strewn with coarse meal, and *Evernia furfuracea*, growing on the bark of old trees, owes its name to the fact that it seems to have been overstrewn with meal.

It has already been stated that the multicellular offshoots (gemmæ or thallidia) of Mosses and Liverworts may be distributed by wind as well as by rain-water. We might mention as examples, *Aulacomnion androgynum*, *Calypogeia Trichomanes*, *Scapania nemorosa*, *Jungermannia bicuspidata*, and *Blasia pusilla*, whose offshoots are borne on special erect supports (see figs. 196 [15, 16, 17, 18], p. 23), or *Syrrhopodon scaber*, which grows in Central America, and whose thallidia are formed on the apex of the leaflets (figs. 196 [12, 13, 14]). The Moss *Tetraphis pellucida* (figs. 196 [4, 5, 6]), which grows commonly on rotten tree-trunks in Pine forests in mountainous regions, might also be mentioned. It develops multicellular disc-shaped gemmæ at the top of certain erect shoots. The discs are supported on delicate filamentous stalks and are embedded in a cup of closely crowded leaflets (figs. 196 [5, 6, 7, 8]). After the supporting threads have withered and the small multicellular discs have become detached, a slight shaking by the wind is sufficient to make the gemmæ fall out and to scatter them. The same breeze which shook the stem now whirls the tiny green discs far over the forest ground and transports them to other places of attachment where they continue their development.

In some Mosses whose little leaves are very brittle when dry, for example, in *Campylopus* (see fig. 196 [11]), the leaves themselves serve as offshoots. How the detachment of these leaflets is brought about is to some extent an enigma; apparently they separate and are thrown off spontaneously, not unlike the foliage-leaves which fall from the branches of trees in autumn. This is immaterial to the question under consideration here, however. This much is certain, that in the remotest mountain ravines, and on inaccessible ledges in precipitous places where the disturbance of passing animals is quite impossible, the turf-forming crowded stems of *Campylopus* always carry detached and partially split leaflets which adhere loosely to the support. When after a few dry days a storm rages through the ravines, these loose leaflets are torn away, and do not again come to rest until they are far distant from the spot from which they were taken. The offshoots of Mosses composed of groups of cells, and the last-mentioned detached leaves which function as offshoots, do not grow up immediately into new Moss-plants, but first of all develop protonema-like cell-filaments, and it is from these that the young Moss-plants originate.

It also happens that whole Moss-plants with elongated axis, numerous leaves,

and abundant rhizoids are distributed by wind. This is observed in Mosses of very different genera (e.g. *Leucodon sciuroides, Thuidium abietinum, Hypnum rugosum, Myurella julacea, Conomitrium Julianum, Anœctangium Sendtnerianum*). The development of this form of offshoot is shown in figs. 156[9] and 156[10], p. 23, in *Leucodon sciuroides*, which is common on the bark of old trees. In the angles made by the leaves with the axis of old shoots, buds first arise which grow into miniature Moss-shoots. These tiny shoots then become loosened at their base, and push up towards the top of the leaves supporting them. This happens more especially in rainy weather. When it is dry their leaflets lie close to the axis, but when saturated with moisture they stand out and bend backwards, and thus raise themselves out of the deep niche in which they have hitherto been concealed. Many of these loosened shoots are without doubt carried away by rain-water, and so transported some little distance, but most of them are whirled off by the wind, and carried far away over mountain and valley.

Bud-shaped offshoots, which become detached from the aërial portions of plants, and whose distribution is effected by wind, are comparatively rare. A remarkable instance is furnished by the Club-moss *Lycopodium Selago* (see fig. 343[2], p. 460). This plant, which is found in mountainous districts in the Northern Hemisphere of the Old and New Worlds, forms buds in the axils of its stiff, dark-green leaves, especially near the top of the shoot, which might, at first sight, be mistaken for small winged fruits. These buds are so provided with little leaves as to offer a good purchase to the wind, and by this means they are transported (*cf.* fig. 343[5]). The North American *Lycopodium lucidulum, L. reflexum, L. Haleakala, L. serratum, L. erubescens*, behave in just the same way as *Lycopodium Selago*, and it is not improbable that many other allied species exhibit this kind of offshoot.

Most detached bud-like offshoots, which develop in the axils of foliage-leaves and bracts on larger plants, *e.g.* on the bulbiferous Coral-wort (*Dentaria bulbifera*; see p. 461), can hardly be said to be distributed by wind. They are spherical or ovate, and not flattened like those of the Club-moss, and they are too cumbrous for transport on the wings of the wind. And yet the wind plays an important part in the distribution in such cases. The bulbils are borne on fairly stiff shoots, and the nature of their attachment is very fragile. Thus, as the shoot rebounds after the blast, many of the bulbils become detached, and are jerked away to a considerable distance.

There are three types of offshoots which are jerked from the plant in the above-mentioned manner. First, those which have the form of closed buds or small bulbs, and which consist of a very much abbreviated stem or bulb-axis, and a few much-thickened scale-leaves filled with reserve materials. These are found in the bulbiferous Coral-wort, which grows commonly in Central European Beech forests, and has been selected as typical; on the bulbiferous Saxifrage (*Saxifraga bulbifera*), widely distributed in meadows in Eastern Europe; on several Lilies (e.g. *Lilium bulbiferum, tigrinum*, and *lancifolium*); and on the Persian *Gagea* (*Gagea Persica*), in the axils of the upper foliage-leaves; on *Foucroya gigantea*, growing in the

Antilles, and above the disc-shaped bracts on the top of the stalk on a considerable number of species of *Allium* (e.g. *Allium Moly, vineale, oleraceum, carinatum, arenarium, Scorodoprasum, sativum*). A second type, growing in the axils of bracts on the upper part of the stem, is shown by *Polygonum bulbiferum* and *viviparum*, natives of the far north, and of the Alpine regions of Europe and the Himalayas (see figs. 452 [1, 2, 3, 4, 5, 6, 7, 8]). These are not bulb-like structures, but small tubers or corms with a minute terminal bud projecting like a little horn, and the tissue of the tuber is abundantly filled with starch and other reserve materials (see figs. 452[9] and 452[10]). The third type is observed in species of the genus *Globba*, belonging to the Scitamineæ, more especially in the East Indian *Globba bulbifera* and in *Globba coccinea*, which grows in Borneo. These rare plants develop offshoots in the axils of bracts on the uppermost part of the rigid stem. They consist of a small bud, from whose minute axis a thick, fleshy root filled with reserve materials grows down, so that in reality the chief part of the offshoot consists of a root-structure.

When the closed bulb-like offshoots, tubers, or buds with thickened roots have been thrown from the wind-swayed stem they remain unaltered in the spot where they have found a resting-place through the whole winter, or the whole dry period of summer. At length, when the most suitable time of year arrives, little absorbent roots make their appearance (see fig. 452[5]) at the expense of the stored-up reserve materials, and these fix the offshoots in the soil and convey fluid nourishment to them. The axis of the offshoot elongates and grows into a stem, putting out leaves and forming a new independent plant.

The entire sprouts, which are detached from aërial stems and become offshoots, can obviously not be transported very far by wind. They are much too heavy, and offer no suitable hold to the wind, which can only influence them by shaking the stem on which they are supported, or by rolling them along after they have fallen to the ground. In the former case the sprout-like offshoots are jerked off, and the action of the wind is therefore only indirect. Some plants bear side by side on the same stem tubers with undeveloped buds, and also some whose buds have begun to grow into sprouts, and have developed green foliage-leaves. These form a connecting-link between the groups just described and those we are now about to consider. One of them is the already mentioned viviparous *Polygonum* (*Polygonum viviparum*, fig. 452), in which it often happens that all possible stages of development occur close together on a single spike.

In Grasses especially it is often the case that the offshoots when ready to be detached have the form of developed, leafy sprouts. In the Grasses of the Arctic flora belonging to the genera *Poa, Festuca*, and *Aira*, the formation of leafy sprouts which become offshoots is so usual that in places the plants bearing offshoots are more common than those bearing flowers in their panicles. On our high mountains also there grows a grass (*Poa alpina, cf.* fig. 342[8], p. 455), in which the panicles as often bear offshoots as flowers. On the plains of Hungary flourishes a species of Meadow-grass (*Poa bulbosa*), in which the same thing happens to such an extent that in the many thousand plants which cover the ground all the panicles develop

offshoots exclusively. The detachment takes place in different ways in these "viviparous" Grasses. Usually the sprouts loosen from the erect panicles of the

Fig. 452.—*Polygonum viviparum.*

[1] Entire plant; one spike bears flowers only, the other carries tubers on the lower half and flowers above. [2] A whole plant whose spike bears tubers only. On some of the tubers small foliage-leaves have already developed. [3–8] Fallen tubers in successive stages of development; nat. size. [9] A fallen tuber magnified. [10] The same in longitudinal section.

swaying haulm, and are scattered by the wind, but sometimes the separation does not occur until the stem is bent down to the ground with the weight of the crowded offshoots in the panicle. In this case the offshoots strike root where the panicle

touches the soil, and the result is that closely-crowded groups of new plants grow up round it. The same thing may be observed in *Chlorophytum comosum*, a native of the Cape often cultivated as a basket plant by gardeners under the name of *Cordyline vivipara*. In this plant leafy shoots are very regularly developed in the floral region instead of flowers, and as these increase in size and become heavier, the long, comparatively slender and very supple stem which bears them sinks down so that the sprouts are suspended on a green thread. If the ground below is suitable the pendent shoots which have meanwhile developed roots may settle there. If they do not come into contact with any suitable soil they remain a long time swaying in the air, growing and themselves forming long, thin stalks in their turn in whose floral region fresh, leafy sprouts with roots arise, and years after three or four generations of shoots connected together by a slender green stalk may be seen hanging down for the length of a metre. At length one or other of the swaying and wind-tossed sprouts strikes firm ground and takes root, separating itself from the old plant, or it falls like the fruit from a tree and rolls down below until it finds a place of settlement possibly at a considerable distance from the old plant.

Among the Rushes also there are many species which develop pendent sprouts. In one species which is very widely spread over Northern Europe, viz. *Juncus supinus*, it is much more usual to find sprout-like offshoots in the floral region than flowers. In many of the Saxifrages of the far North, viz. in *Saxifraga stellaris*, *S. nivalis*, and *S. cernua*, very reduced shoots with small rosettes of foliage-leaves are formed on the terminal branches of the floral axis, or bulb-like buds arise in the axils of the bracts on the upper part of the stalk which, like those of the viviparous *Polygonum*, send out green foliage-leaves before they fall or become loosened (see figs. 342 [1, 2, 3, 4, 5, 6, 7, p. 455). *Sedum villosum*, which grows on moors, develops short, leafy sprouts with thread-like axis in the axils of the stem-leaves. As soon as the stem begins to wither these sprouts loosen and are carried to a short distance by gusts of wind. They send out delicate roots as soon as they find a resting-place and new plants are established.

A very peculiar mode of detachment and distribution of sprout-like offshoots is found in many species of House-leek (*Sempervivum*). The *Sempervivum soboliferum* illustrated here may be taken as an example. The thick, fleshy leaves of this plant are arranged, as in all House-leeks, like rosettes on abbreviated axes, and the new rosettes are always laid down as minute buds in the axils of the rosette-leaves. From these buds proceed thread-like runners, furnished with small adherent scales, ending in a reduced shoot. The crowded leaves of this reduced shoot enlarge, forming a small rosette, the leaves being folded so closely together that the whole structure has a spherical form. For some time the round rosette is nourished by means of the filamentous runner from the old plant, but afterwards the runner withers and dries up and the rosette breaks away from it. It is now quite separated from the parent plant (see fig. 453). A gentle breeze is sufficient to roll along the small detached balls; and as the House-leeks in question choose

as their habitat narrow ledges in rocky places, it is inevitable that some of the separated rosettes should fall over the steep wall, and should not come to rest till they have travelled a considerable distance from the mother-plant. Roots are soon developed from the base of the detached rosettes, by which they become fixed to the substratum. Usually a parent plant produces 2–3 rosettes, but frequently as many as six, and the neighbourhood of the terraces overgrown with the species of House-leek figured, and with other allied species (*Sempervivum arenarium*,

Fig. 453.—*Sempervivum soboliferum*. On the lower step of the rock lie five ball-shaped offshoots which have become detached from the upper rocky platform and have rolled down. The butterfly and snail are introduced into the picture to show the true proportions of the offshoots.

S. Neilreichii, S. hirtum) often looks as if it had been sown with the ball-like rosettes, which have rolled down

Sedum dasyphyllum (see fig. 454 [1]), which grows in rocky crevices and in the niches of old stone walls, develops offshoots partly in the floral and partly in the foliage region. In the floral region the offshoots originate by the metamorphosis of floral-leaves into foliage. Instead of flowers there are small rosettes (fig. 454 [5]) of thick, ovate, green scales, like those which take the place of flowers in *Saxifraga nivalis* and *S. cernua* (*cf.* p. 455). These rosettes in the autumn break away from the flower-stalks, and behave just like those of *Sempervivum*. In the foliage region the offshoots arise in three ways. In the axils of the uppermost leaves there is formed a bud which is hardly perceptible to the naked eye. It is embedded in the

shallow depression on the upper side of the thick leaf, and possesses 2–3 leaflets about ·5 mm. in diameter (fig. 454[2]). In the axils of the lower foliage-leaves short sprouts are formed, whose axes are furnished with fairly large crowded rosette-shaped leaves (fig. 454[3]). In the axils of the lowest arise rudimentary sprouts, with an elongated thread-like axis bearing 8–14 thickly-crowded leaflets at its end (fig. 454[4]). As soon as the stem carrying the flowers begins to wither, the foliage-leaves and the buds or sprouts in their axils loosen from it and fall to the ground. The succulent, very turgid, almost hemispherical leaves are comparatively heavy, and if the spot where they first fall is sloping they do not lie still, but roll down until they are caught by some projecting ledge, or a mossy cushion, or arrive on level ground. Since they carry with them the buds and sprouts formed in their axils, they to a certain extent function as a means of transport. As soon as the offshoots come to rest, they develop rootlets at their base at the expense of the reserve materials of the detached succulent leaf. Rootlets are often formed even while the leaves are still adhering to the decaying stem. It is worthy of note that the aqueous tissue of the fallen leaves also plays a part in the establishment of these offshoots. If the spot where they have come to rest is exceptionally dry, as is usually the case in places where *Sedum dasyphyllum* grows, the supporting leaf may for a long time provide the water necessary for the maintenance of the offshoot, and so protect it from perishing.

Fig. 454.—The formation of offshoots in *Sedum dasyphyllum*.

[1] Entire plant; nat. size. [2], [3], and [4], Offshoots which have developed at different levels on the stem in the axils of the leaves. [5] Offshoots from the floral region.

The formation of sprout-like offshoots is very remarkable in the Kleinias, natives of the Cape, which belong to the Compositæ. Some species of this genus, viz. *Kleinia neriifolia* and *K. articulata*, remind one very much in their appearance of certain Cacti. The fleshy, much-thickened cylindrical branches are connected with one another by thin strands, and the whole plant looks as if it had been constricted at intervals by ligatures. The strands joining the heavy cylindrical branches break at the slightest pressure, and the upper shoots especially may be broken off even by a violent gust of wind. The result of the fracture at the constricted places, however, is that the branches fall to the ground. If the plant grows on a slope, the fallen cylindrical shoots roll down until they are stopped by a projecting stone or some other obstacle. When they come to rest they develop numerous roots

where they touch the ground, and at the same time send up new lateral branches from the opposite side, as shown in fig. 455. It should be mentioned that in *K. articulata* the roots often begin to develop before the branches have broken and fallen off, always appearing on the side of the shoot which is turned towards the soil. This also is shown in the figure.

Fig. 455.—The formation of offshoots in *Kleinia articulata*.

In all these instances the offshoots are detached by the force of the wind. Another method by means of which the same end is attained depends on the hygroscopic properties of the tissues concerned, and on the alternate swelling and contraction from this cause. Several Fungi of the group Peronosporeæ, among others the unwelcome Potato-disease Fungus, *Phytophthora infestans*, multiply by spores formed on delicate hyphal threads, which are protruded from the stomata of the

host plant. These hyphal threads bifurcate, and the end of each branch swells up into a spore. The supporting hyphal branch then grows out again below each spore, elongates, and extends upwards, and pushes the spore on one side. The result of this oft-repeated process is a structure which resembles a small much-branched tree, with egg-shaped fruits hanging from the boughs. The hyphal branches, on which the spores are set like fruits, are cylindrical, stiff, and turgid in damp air, but in dry air, especially when they are ripening, they become ribbon-like and spirally twisted so as to resemble cotton-cells. They are extremely hygroscopic, and the slightest change in the humidity of the surrounding air is enough to increase or diminish their spiral torsion. Even mere breathing on them produces an alteration in the twisting, and if a rapid and marked alteration occurs in the hygroscopic condition of the environment, the branches with their hanging spores are whirled hither and thither, and the spores, which are only attached but slightly, are scattered in all directions. This cannot of course be seen except under unusually favourable circumstances, on account of the minuteness of the spores.

The shedding of the spores can be observed with the naked eye in the Mould *Pilobolus cristallinus*, one of the Mucorineæ, shown in figs. 456[1] and 456[2]. The mycelium of this Mould consists of a colourless, much-branched tube, and grows on the excrement of horses and other mammals. Enlargements arise on the mycelium, and from each is produced a sporangial mechanism composed of two parts, a colourless, barrel-shaped, stalk-cell and a dark head. The latter contains a colourless jelly, which swells up in water, together with numerous spores, and is to be regarded as a sporangium. Its wall is covered with calcium oxalate, so that its elasticity is completely lost and it becomes brittle. The cell-wall of the barrel-like swollen stalk, however, remains soft and elastic. At the junction of the dark sporangium with its colourless stalk a circular layer of separation is formed. When the turgidity of the sporophore increases in consequence of the absorption of water from the mycelium the tension at last becomes so great that it causes a rupture round the circular line mentioned. At the same moment, however, the elastic wall of the part of the sporophore immediately below contracts, and the fluid contents are pushed out with great force. The push is transmitted to the dark sporangium above the split, and both the fluid contents of the club-shaped support and the entire sporangium are thrown off (see fig. 456[2]). The force of the explosion is so considerable that the dark mass is raised about a metre in height. The whole process, which, as we have said, may be seen with the naked eye, usually occupies 18–20 hours. The development of the mechanism begins at mid-day; during the night the spores are formed in the vesicle, and the next morning the explosion occurs as soon as daylight appears.

A no less interesting spectacle is afforded by the scattering of the unicellular offshoots, *i.e.* conidia, in species of the genera *Empusa* and *Entomophthora*. These live on the dead bodies of caterpillars, flies, aphides, and other insects, the commonest and best known being *Empusa muscæ*, which lives on the common house-fly. When a conidium of this *Empusa* falls on the body of the fly it puts out a tube which pene-

trates into the body-cavity, and there it divides up repeatedly, forming numerous cells throughout the body. The infected fly, sickening under the injurious influence of the Fungus and almost at the point of death, seeks for some quiet spot in which to die. It frequently chooses for its last resting-place a window pane, in which case it is possible to thoroughly investigate the further development of the Fungus. After the death of the fly the round cells of the *Empusa*, hitherto hidden in the body-cavity, grow out into long tubes which pierce the skin of the fly's corpse and appear as short club-shaped structures on the surface. A single egg-shaped conidium

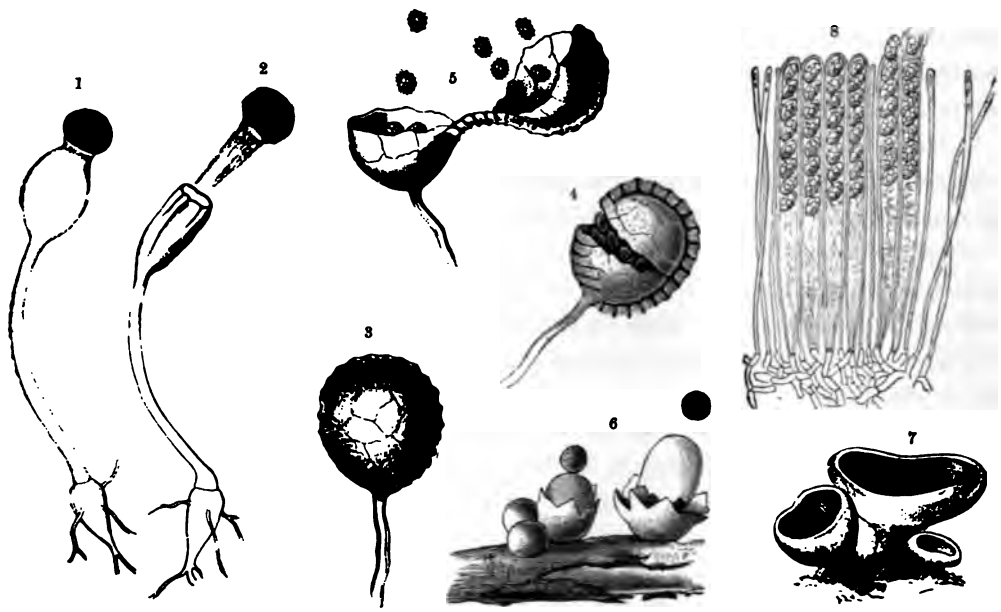


Fig. 456.—Distribution of spores by expulsive mechanisms.

[1] *Pilobolus crystallinus* before the sporangium breaks away. [2] The same at the moment when the sporangium is thrown off. [3] Sporangium of *Nephrodium Filix-mas* closed. [4] and [5] The same in the act of splitting and scattering the spores. [6] *Sphærobolus stellatus* at the moment when the balls filled with spores are thrown off. [7] *Peziza aurantia*. [8] Longitudinal section through this *Peziza*. The spores are escaping from two of the asci. All the figures magnified

is then cut off from each club-like end of the tube, and this is thrown off in exactly the same way as the sporangium of *Pilobolus* (*cf.* fig. 383[7], p. 672). Here, too, a place is formed for the splitting, and here again the mucilaginous contents are thrown off simultaneously with the conidium by the sudden contraction of the club-shaped end of the tube, and the conidium is thus always surrounded by a gelatinous adhesive mass (fig. 383[8]). The distance of the projection may be as much as 2–3 cm., which, considering the extraordinary minuteness of the conidia, is proof of great power. The dead fly then appears to be surrounded by a veritable halo of detached conidia which are firmly attached to the substratum (fig. 383[6]). This is to be accounted for by the fact that, as already stated, a part of the sticky mucilaginous contents of the club-shaped end of the tube are thrown out with the conidia. This serves as an adhesive material, and causes the conidia to adhere particularly firmly to glass window panes. If a living fly which happens to be near is struck by the projected

conidia, they stick to it so firmly that it cannot succeed in getting rid of them or freeing itself in spite of all its attempts. Each adhering conidium then again sends a tube into the body-cavity of the fly, and the development is repeated in the way just described. The same thing happens in *Entomophthora radicans*, which lives on the caterpillar of the Common White butterfly (*Pieris Brassicæ*). It is represented in figs. 383 [1, 2, 3, 4, 5], p. 672). Tufts of delicate thread-like hyphæ come out of the body of the caterpillar for the purpose of forming conidia (fig. 383 [3]). These gradually form a thick web round the dying caterpillar, and at a cursory glance one might think it had woven its covering and changed into a chrysalis (fig. 383 [2]). The tubes, looking like fine threads, unlike those of *Empusa*, are here much-branched, and actual tufts of hyphæ arise from whose ultimate somewhat swollen ends the long, sticky conidia are abstricted and scattered (figs. 383 [4] and 383 [5]).

The scattering of the spores from the asci of Ascomycetes takes place in a characteristic manner. They are developed in groups of 2, 4, 8, 16, or 32 in the tubular asci, and numerous thread-like hyphal ends, the so-called paraphyses, occur between the asci (see fig. 456 [8]). In addition to the spores the asci contain protoplasm and cell-sap, and are considerably distended by the large amount of the latter. As the dilatation increases the asci burst, and their cell-wall, which is at a high tension, exercises a powerful pressure on the cell-contents, which are extruded with great force. The place where the rupture of the wall of the ascus occurs is determined beforehand, so that the extrusion of the cell-contents and spores always takes place in the same way. In many species the top part of the ascus-wall is raised like a lid, in others a transverse splitting occurs, and in others again the spores are ejected through a small circular hole. A slight shake or a dry breeze is quite enough to cause the ejection, and in *Spatularia flavida*, for example (figured on p. 791), or in *Peziza aurantia* (see fig. 456 [7]), it is easy to observe how small clouds of extruded spores rise from the surface of the fructification as soon as these Fungi are brought from a damp place into a dry atmosphere, or when a dry wind blows over them. In some species of *Ascobolus*, minute black or waxen yellow Fungi living on the excrement of animals, the spores are not only ejected, but the turgidity of the tissue surrounding the tubes is so great that the whole tubular layer is extruded with the spores.

Some Gasteromycetes have special contrivances for scattering the spores. In species of the genus *Geaster* (see figs. 391 [4] and 391 [5], p. 690) the threads of the capillitium and the spores imbedded between them develop within a tough, leathery, bladder-like envelope which separates into two layers when the spores are ripe. The inner layer has the form of a bladder, and opens only at a spot at the apex. The outer layer, on the other hand, splits into 4–12 radiating lobes. The position of the lobes alters remarkably according to the hygroscopic condition of the atmosphere. In damp weather they fold together over the vesicle, but in dry weather, especially in sunshine and when a dry wind is blowing, they bend back so forcibly that some of the spores are shaken from the mouth of the vesicle. Travellers in Central America tell us of the gigantic Puff-balls which literally explode on being

shaken, sending such quantities of reddish spores into the air that it is impossible to breathe in their vicinity. In Europe a minute Puff-ball, *Sphærobolus stellatus* (fig. 456 [6]), grows on decaying stems, leaves, &c. The wall of the fruit divides, as in *Geaster*, into two distinct layers: one remains closed and assumes the form of a ball, but the outer one when the spores are ripe divides by radiating clefts into several lobes. These bend back rapidly on drying, and as the central portion round which the lobes are placed becomes strongly arched upwards, at the same time the ball containing the spores is shot out with considerable force.

The dissemination of spores in some of the Ferns is illustrated in figs. 456 [3, 4, 5]. Sporangia are developed on the under surface of the frond, where they are arranged in various ways. Those of the *Nephrodium Filix-mas*, which is here selected as a type, consist of a stalk and a flattened bi-convex vesicle. Round the latter runs a ring of darker-coloured cells, whose side-walls are much thickened, while their outer walls remain thin and delicate. When the sporangium is ripe its bursting is brought about by the contraction of the cells of the ring.

With regard to the distribution of offshoots by animals we may distinguish two classes, those in which the offshoots are first conveyed to the animals by special disseminating mechanisms, so that two methods of distribution are combined, and, secondly, those in which animals alone effect the transport of the offshoots from one place to another. We have already spoken repeatedly of the former class. Of the latter the distribution of spores by food-seeking animals is the first to be considered. The Pyrenomycetous Fungus known as the Ergot of Rye (*Claviceps purpurea*) is a well-known instance. The thick web of hyphal threads which invests the ovaries of the Rye is penetrated by labyrinthine passages, whose walls are formed by the ends of hyphal threads arranged in rows and tufts (see fig. 386 [2], p. 680). Spherical spores are abjointed from these somewhat club-shaped ends. Simultaneously with this abjunction the outer layer of the cell-wall of both spores and hyphæ forms a sugary fluid by the absorption of water and subsequent breaking down. This fills the winding passages, and the innumerable abjointed spores are imbedded in it. The sweet-tasting fluid gradually collects into drops on the exterior, and even comes into view on the spikes of Rye between the glumes which surround the infected ovaries. This is the "honeydew" by which the presence of the parasitic *Claviceps* in the interior of the spike is recognized, and which is viewed with some apprehension by the farmer. Insects, especially wasps and flies, eagerly seek out these springs of sweet fluid and suck and lick up the juice, which is crowded with numberless spores. It is therefore inevitable that small quantities of spores should stick and remain hanging to portions of their bodies, and when they fly to the spikes of other Rye-plants the spores are easily rubbed off, and in a very short time may again grow up into a mycelium involving the ovaries there.

A similar phenomenon may be observed in the Phalloideæ, belonging to the Gasteromycetes, of which the best known species, the Stink-horn Fungus (*Phallus impudicus*), may be taken as an example. The cap, borne on a white cylindrical and spongy stalk, is bell-shaped and covered with a greenish-black viscous fluid in

which numerous spores are imbedded. This fluid gives off a far-reaching carrion smell which allures many insects, especially carrion-flies. The fact that the fluid contains sugar which serves as nourishment for the insects also contributes to the allurement. A fly which alights on the cap of the Stink-horn cannot leave it without spores adhering to its whole body. Some of them may, perhaps, fall off while it is flying away, but the majority will not be brushed off until it again alights and cleanses itself from the uncomfortable appendages (*cf.* also p. 691).

It is well known that the fleshy fructifications of Hymenomycetes provide food for numerous insect-larvæ. Frequently as soon as the receptacles appear above the soil the flesh of the stalk and cap are riddled by passages in which live the larvæ of various gnats and beetles. These leave their dwellings before the decay and decomposition of the Fungi set in, and enter the chrysalis stage in the ground. In this way numerous spores which have adhered to the animals are carried away and disseminated. The spores of various Fungi, especially of the Hymenomycetes and Truffles, are without doubt distributed by animals which eat the fleshy spore-bearing portions. The spores pass unharmed through the alimentary canal and then germinate in the deposited excrement. Earthworms and swine in particular seem to take part in this distribution.

The dissemination of detached bud- and shoot-like offshoots is comparatively seldom effected by animals. Of the cases known the following are the most noteworthy. First, where the offshoots are taken up as food by animals, but are again got rid of in an undigested condition, and grow up into new plants in the place where they have been deposited. This has certainly been observed in *Polygonum viviparum*, which grows commonly in the far North and on the high mountains of Central Europe (see fig. 452). The bulbils of these plants are a dainty morsel to ptarmigan, and are eagerly sought for by them. The ptarmigan seizes the lower half of the spike of the Polygonum with its beak, and by a quick movement of its neck passes the bill the whole length of the spike, and so puts dozens of bulbils at a time into its crop. Numerous observations have shown that the bulbils of *Polygonum viviparum* and cranberries are the commonest food found in the crops of ptarmigan shot on the Alps, and I also always found these bulbils in great quantity in the crops of Norwegian ptarmigan. The portion which passes from the crop into the muscular gizzard is of course crushed and digested, but it has often been noticed that part of the food so greedily swallowed by the ptarmigan is thrown up again, and this is particularly the case with the bulbils when they have been taken in excess. When thus extruded, they have the power of further development; far from being destroyed, they grow up very rapidly into new plants, and as the places where the superfluous food is thrown out are always at some distance from the spot where the ptarmigan obtained the bulbils, this process is really a mode of distributing the *Polygonum viviparum*.

The second method of distributing detached offshoots by animals is effected by means of barbed bristles and hairs, such as are represented in fig. 457, in the Mamillarias (*Mamillaria placostigma* and *gracilis*) of the high mountains of Mexico.

Here some of the spherical, closely-crowded lateral shoots growing from the old plant loosen spontaneously and fall to the ground; others again remain *in situ* but adhere very slightly, so that a passing contact or a gentle touch is enough to complete the separation from the old plant. Now bristles are formed at the top of each papilla of these Mammillarias, some of which end in barbs, so that the spherical shoots resemble burs. They adhere just like burs to the hairy paws or fur of grazing animals, which carry them away unconsciously. Afterwards

Fig. 457.—Distribution of detached sprout-like offshoots by means of animals.

1 *Mammillaria pkacostigma.* 2 *Mammillaria gracilis.*

the animals when resting seek to rid themselves of the inconvenient appendages, brushing them off and leaving them behind on the ground. Here they may strike root and grow up into new plants.

The third method of distribution of sprout-like offshoots by animals is seen in aquatic plants, which fasten either entirely or in fragments to passing water-birds. Certain species, which very rarely blossom or form fruit, but nevertheless occur in innumerable widely distant spots and often appear unexpectedly in newly-formed ponds, in artificial lakes, and in other waters, are for the most part distributed by water-birds. Some of these water-plants, *e.g.* the Frogbit and Bladderwort (*Hydrocharis* and *Utricularia*), develop peculiar slimy coverings round their buds, which

cause them to stick to the feathers of birds which come in contact with them as they swim by. Others, such as the small Duckweeds (*Lemna minor, gibba, polyrrhiza*), hang by their long, somewhat twisted, floating roots, and many filamentous Algæ, *Aldrovandia*, the delicate Riccias (*Riccia natans* and *fluitans*), the Ivy-leaved Duckweed (*Lemna trisulca*), &c., become attached in their entirety to the coot and duck swimming in the ponds and lakes. These fly away with them, but as soon as they again enter other water the adhering plants fall off or are cleaned off by the birds, and in this way they are distributed quite fresh and living over great distances. We might also mention in this connection the peculiar distribution of Ulvas, Florideæ, and Sea-wracks by means of crabs, which was described at vol. i. p. 77.

We will only allude in passing to the fact that many economic plants are propagated and distributed by offshoots to a very great extent by man. Bananas whose fruits contain no fertile seeds, Potatoes, Artichokes, and many other tuberous and bulbous plants are continually multiplied by the help of slips, tubers, bulbs, &c. The intentional artificial propagation by offshoots has of course no apparent influence on the development of a natural method of distribution in such species. Although planted and cultivated in large quantities they do not become naturalized; and if it were not for the artificial maintenance and propagation by offshoots they would soon vanish again from such places, leaving no trace behind. This is, however, not the case with the unintentional distribution of offshoots of certain plants by man. The keels and bottoms of ships journeying over wide seas become, like the stakes and buoys of the harbour and the sea-walls and rocks of the shore, quite overgrown with sea-weeds. If these are removed by chance or intentionally from their substratum they do not necessarily perish. They may remain alive in the sea-water, and under favourable conditions may attach themselves to some other firm spot of ground. In this way plants may be transmitted from one coast to another over very wide distances. Another unintentional distribution of plant-offshoots by man occurs on cultivated ground in vineyards, fields, and gardens. By ploughing, digging, and throwing up the soil the bulbous or tuberous offshoots embedded in the ground undergo a change of position. The offshoots of certain plants may in this way be distributed so uniformly over a whole field by spade and ploughshare in the course of a year that it almost looks as if they had been purposely planted there. It is curious on journeying through the vine-planted districts of Northern Italy to see one of two adjacent vineyards abundantly covered with wild Tulips, while not one is visible in the other. In Central Europe the same thing happens with the Gageas (*Gagea arvensis, G. stenopetala*) growing in the fields, and with the tuber-forming Earth-nut pea (*Lathyrus tuberosus*). One field looks as if it had been sown with Gageas and yet its neighbour is completely devoid of them. On the Günselhöhe in the Lower Austrian Erlafthal I once saw a rectangular ploughed field overgrown from one end to the other with plants of the Bulbiferous Lily (*Lilium bulbiferum*), while only isolated specimens of this plant could be seen in the adjoining fields. There is no doubt that here the bulbils thrown on to the ground from the

leaf-axils of a few plants had been distributed equally by ploughing over the whole field, although this distribution had certainly not been intended by the ploughman.

It would of course be a mistake to explain the uniform distribution of bulbous plants over a large stretch of land exclusively by the ploughing and overturning of clods of soil full of bulb-like offshoots. In many instances the distribution of such offshoots is also produced by the pulling action of the roots. This process is so remarkable that we must describe it somewhat in detail. The multiplication of subterranean bulbs is known to take place by the formation of buds in the axils of the scale-leaves, and these, in the course of a few months, themselves grow up into small bulbs. When mature, they may form the termination of a slender shoot which, of course, never attains any considerable length, but which in many cases is thread-like, as shown in *Muscari racemosum* (fig. 444[1]). The small bulbs are pushed by this thread-like shoot out of the region of the protecting scale-leaf near the old bulb, and there they develop long root-fibres in abundance. In other instances the shoots remain extremely short, and the small bulbs are not pushed out, but the protective scale-leaf, in whose axil they originated, decomposes, and they send out their roots through the decomposing tissue into the surrounding soil. In both cases they become detached at the end of the vegetative period in which they originated; they are then no longer connected with the old bulb, but are quite independent. Many species form only one bud in the axil of a bulb-scale, others a whole series which all grow up into bulbs; in the latter case the old bulb in the autumn is surrounded by a whole family of small young bulbs. There is a species of Garlic called *Allium pater-familias* whose old bulb gives rise to about a hundred young ones in a year. It is impossible for so many to develop properly when closely crowded together round the plant from which they sprang; mutual pressure would be unavoidable in their further growth, and if next year each of these bulbs should in its turn form new offshoots, and again become the centre of young bulbs, it would become imperatively necessary to make room, and to thin and separate the dense crowd. Since all the bulbs are placed with their apices pointing upwards they cannot be moved apart by the elongation of their stems; the mutual pressure of neighbouring bulbs as they enlarge would certainly cause a trifling displacement, but this would not prove an efficient remedy. The remarkable pull of the roots, which was described in vol. i. p. 768, now comes into play. Only a few of the roots arising from the base of a young bulb strike downwards; by far the greater number grow out at a right angle to the axis of the bulb in a direction parallel with the surface of the soil (see fig. 444[1]). When these very long roots have stopped growing they contract, and thus draw the young bulb to which they belong away from the old one. The young bulbs now form a wide open wreath round the old one (which has meanwhile disintegrated), and thus obtain sufficient room for further development. This happens not only in the *Muscari* described, but also in *Ornithogalum nutans*, *Tulipa sylvestris*, and indeed in quite a number of bulbous plants. Since this process is repeated annually a fairly wide area of soil may in the course of years be covered with the bulbs in spite of the slight distance through

which they have been shifted under the ground. Some soil containing bulbs of *Tulipa sylvestris* was once put in a garden in Vienna in the middle of a grass plot shaded by Maple-trees. As the grass was mowed every year before the flowers opened there was no formation of seed, and the Tulips could only multiply by offshoots. After about 20 years the lawn was covered with Tulip-leaves, which arose from subterranean bulbs occupying an area 10 paces in diameter. Thus in the time mentioned the bulbs had spread for about 5 paces in all directions, in consequence of the pull of the contracting roots. It is more than probable that the offshoots of many perennial plants with erect stem and napiform or tuberous roots, *e.g.* the blue-flowered species of the Monkshood (*Aconitum Napellus*, *A. Neubergense*, *A. variegatum*) undergo a change of position by the pull of their horizontal root-fibres; and that the clustered arrangement of these plants is the result of the root-pull.

A review of the very varied modes of origin and distribution of offshoots leads to the conclusion that they may be formed on all parts of the plant, that the form of the offshoot is constant for each species, or, in other words, that the form of the individual parts of the offshoot in succeeding generations is repeated as exactly as the flowers and fruit, but that one and the same species may frequently form two or even three kinds of offshoots. The Fungus *Claviceps purpurea* develops spores which are distributed by honey-sucking insects, also the sclerotia known as "ergot", which are scattered from the dry spikes by the swaying movement of the stem, and thirdly, filamentous spores, which are extruded from asci, and distributed by wind. The Liverwort *Blasia pusilla*, develops thallidia in special flask-shaped receptacles on the surface of the thallus, and spores in the sporogonia. The form of the offshoot is always adapted to the season and to the distributive agents available where they are formed. In one case it is more suitable that the offshoots should be distributed slowly, and step by step, in another quickly and by bounds. In the spring it may be more advantageous if they are distributed by wind, by animals in the summer, and by self-scattering mechanisms in the autumn. Steppe-plants must develop different offshoots from those formed by plants living on the damp, shady floor of the forest. It is just as obvious that offshoots, which creep along, above, or under the ground without leaving the soil, must be equipped quite differently from those which are detached from their place of origin, and either roll along or are carried by wind, or have to travel long distances as the appendages of wandering animals. In the former, it is all-important that they should be able to overcome possible obstacles in the soil; in the latter, that they should not perish during their journey for lack of food and water. When separated from the soil they are greatly exposed to the danger of drying up, and even when they have settled somewhere, the supply of water they require for the formation of organs of attachment and absorption is by no means assured. Settlers of this kind must either be so organized that they can sustain a long-continued drought without injury, like the offshoots of the Mosses and the soredia of Lichens, or they must themselves bring with them the necessary water supply, and care must be taken

that this supply is not lost prematurely by evaporation. As a matter of fact, such detached offshoots, *e.g.* those of *Sempervivum*, *Sedum*, *Kleinia*, or *Mamillaria*, are not only provided with a special aqueous tissue, but also with a cuticle which is very effective in preventing excessive transpiration. All offshoots, when liberated from their place of origin, are also provided with the necessary reserves, *i.e.* constructive materials, so that immediately after settling, they can send out absorbent roots and green leaves of their own initiative, obtain a firm footing in their new locality, and extract nourishment from it. When the offshoots are distributed by water-currents, they require neither an aqueous tissue nor protection against drying up, and it may be due to this fact that detached offshoots are relatively more frequent in aquatic than in land plants and lithophytes.

THE DISPERSION OF SPECIES BY MEANS OF FRUITS AND SEEDS.

On the heights of the Kahlenberg, at Vienna, at the edge of the wood, grows an under-shrub which bears the name of *Dorycnium herbaceum*. It is one of the Papilionaceæ, and develops spherical one-seeded fruits, which ripen in October. I once collected from this plant several twigs laden with fruit, for the purpose of a comparative investigation on which I was engaged, and brought them home and laid them on my writing-table. Next day as I sat reading near the table, one of the seeds of the *Dorycnium* was suddenly jerked with great violence into my face. Shortly afterwards I saw a second, third, fourth, and ultimately about fifty seeds let fly from the small clusters of fruit, and each time I heard a peculiar sound which accompanied the bursting open of the fruits and ejection of the seeds. The rays of sunshine from the window had evidently heated and dried the fruits, and occasioned this surprising phenomenon. The incident reminded me of the following passage in Goethe's *Travels in Italy*:—"I had brought home several seed-capsules of *Acanthus mollis*, and put them away in an open box, when one night I heard a crackling noise, and immediately afterwards a sound like the impact of small bodies against the walls and ceiling. I could not understand it at first, but found afterwards that my pods had burst and scattered their seeds all over the place. The dryness of the room had caused the fruits to ripen in a few days to the requisite degree of elasticity."

The fruits of *Dorycnium* and *Acanthus* may be taken as types of a large group designated by the name of Sling-fruits. It is found that when these fruits are ripe, the tissue around the seeds becomes highly tense. The first result of the tension is that the tissue is rent at particular spots, and this rupture is followed by a sudden contraction of the segments, which double back and roll up, at the same time expelling the seeds resting upon them. Sometimes the rolled parts of the fruits, and, more rarely, the entire fruits themselves, are jerked off simultaneously with the seeds. There is the greatest variety in this respect, but all the contrivances for expelling seeds resemble one another in the fact that through their agency the seeds reach places beyond the range of the mother-plants.

In one class of expulsive fruits the high degree of tension which finally results in the disruption and rolling up of particular tissues is caused by a swelling up of the cell-membranes or by the turgidity of the cells. One of the most curious instances is that of the Squirting Cucumber (*Ecballium Elaterium*), which is shown in fig. 458[1]. This plant belongs to the Cucurbitaceæ and its fruit resembles a small fleshy cucumber beset with bristles and borne by a hooked stalk. The end of the stalk projects into the interior of the fruit like a stopper. When the seeds are quite

Fig. 458.—Sling-fruits.

[1] *Ecballium Elaterium*; branch bearing flowers and fruits. [2] A fruit detached from its stalk and with its seeds squirting out. [3] *Oxalis Acetosella*; entire plant with one unripe fruit on a hooked stalk, and one ripe fruit on an erect stalk ejecting its seeds; nat. size. [4] Unripe fruit of *Oxalis Acetosella*; ×6. [5] Ripe fruit of *Oxalis Acetosella* ejecting the seeds; ×6.

ripe the tissue surrounding them is transformed into a mucilaginous mass. Also the tissue in the neighbourhood of the conical stopper just referred to breaks down at the same time, and thus the connection between the stalk and the fruit is loosened. In the wall of the fruit there is a layer of cells which is under great tension, and endeavours to stretch itself out. As long as the fruit is unripe such expansion is prevented by the tense tissue close to the stalk, but with the ripening of the fruit this obstacle is removed. The fruit then severs itself from the conical end of the stalk and at the same moment the expansion of the strained layer of tissue takes place. The consequence is that the interior of the fruit is subjected to great pressure, and the seeds, together with the surrounding mucilage, are squirted out

with considerable force through the hole which was previously closed by the end of the stalk (see fig. 458 [2]).

The Dorsteniaceæ behave in a manner no less remarkable. As in the case of Figs so also in these plants, numbers of small flowers are seated upon an enlarged receptacle, which remains fleshy and succulent after the small one-seeded fruits have developed from the flowers. The lower portion of each fruit has thick walls, and is embedded in the receptacle like a hair-follicle in the human skin, whilst the delicate-

Fig. 459.—Sling-fruits.

[1] *Orobus vernus.* [2] and [3] *Geranium palustre.* [4] *Viola elatior.* [5] *Cardamine impatiens.* [6] *Impatiens Nolitangere.* [7] and [8] *Acanthus mollis.* [9] and [10] *Ricinus communis.*

coated portion projects above the receptacle in the form of a papilla. When the seed is quite ripe the turgidity of the outer cellular layer of the thick wall of the fruit increases, the thin-walled top is torn, the thick walls suddenly close, and the seed hitherto enveloped by them is violently ejected.

A special case of the expulsion of seeds as from a sling is also found in Oxalidaceæ, of which the common Wood-sorrel (*Oxalis Acetosella*, see figs. 458 [3, 4, 5]) may be taken as an example. In this case it is the seed-coat that possesses a special tumescent tissue adapted to the expulsion of the seeds. One of the deeper layers of the seed-coat is composed of tense cells and is itself in a highly strained condition,

whilst the outer layers of cells of the seed-coat are not in a state of tension. When the seed is quite ripe the cell-membranes in the strained layer of tissue swell up, the outer layer of the pericarp, being no longer able to withstand the pressure to which it is subjected, is rent asunder and the edges of the slit thus formed roll suddenly back. A violent jerk is given to the inclosed seed, in consequence of which it flies out through the fissure in the capsule immediately in front of it (fig. 458[5]). The fact of the ejection of the seeds of Balsamaceæ also has long been known. The fruit of *Impatiens Nolitangere*, one of the members of that family, is an oblong capsule composed of five carpels (see fig. 459[6]). The walls of this capsule are constructed of three layers of cells. The layer lying immediately beneath the epidermis consists of large and highly turgid cells, and is called the turgescent layer. It is in a state of great tension, and when the seeds are ripe and the union between the five carpels gives way along the lines of union, a relaxation of the tension takes place, the loosened tissue of those lines is torn, the five carpels roll up, and their rapid movements of involution result in the expulsion of the seeds contained in the fruit. *Cyclanthera explodens* and *Thladiantha dubia*, plants belonging to the Cucurbitaceæ, as also several Crucifers of the genera *Dentaria* and *Cardamine*, in particular the species shown in fig. 459[5] (*Cardamine impatiens*), exhibit similar phenomena, except that in these cases the carpels do not roll inwards but outwards.

In the instances hitherto dealt with the cause of the expulsion is the turgidity of cells or the swelling up of cell-membranes with a concomitant maintenance of a state of extreme tension in a particular layer of tissue situated in the wall of the fruit. In the next class of cases the phenomenon depends on the desiccation and consequent contraction of a special layer of the fruit-wall which leads to a rupture and subsequently to a bending over and rolling up of particular parts of the fruit. This change is accomplished with great rapidity and has the effect of hurling away the seeds or the separate parts of the fruit or even the entire fruit itself. We will only mention some of the best known instances of this kind.

The fruit of the Marsh Crane's-bill (*Geranium palustre*; see fig. 459[2]) has a 5-angled column rising up in the centre of a circle of five carpels. The carpels are hemispherically inflated at the base, and terminate above in long bristles or beaks. Each contains a single seed. When the seeds are ripe, the tissue composing the beaks undergoes desiccation, which, however, is not of uniform intensity throughout. The outer layer, consisting of several plates of succulent cells, dries up more quickly than the inner layer, which is composed of thick-walled cells. The result is that the beak lifts itself away from the axial column, and curls up externally like a watch-spring. No resistance to this movement is afforded by the delicate dried tissue which has hitherto served to hold the carpels together, and as the cavity of each carpel is open along the inner surface, and the seed lies in it simply as though it were resting in the hollow of a hand, the rapid drawing up of the beak has the effect of ejecting it in a wide curve away from the carpel (see fig. 459[3]). In the Marsh Crane's-bill, as also in the other large-flowered species of the genus *Geranium*, the tops of the beaks continue attached to the axis, and the latter, together with the five

empty and rolled-up carpels, resembles a chandelier in shape (shown to right of fig. 459[3]).

Those Violets which have aërial stems, such as *Viola elatior* (see fig. 459[4]), develop capsular fruits, each of which resolves itself into three valves when it bursts open. The valves are boat-shaped, and the marginal parts which form the sides of the boats are thin, whilst the keels are very thick and swollen. Inside each boat, near and parallel to the line of the keel, are two rows of seeds. The valves themselves have an exceedingly complex structure. A cross section through one of them shows a layer of thin-walled parenchymatous cells, a layer of elongated curvilinear cells, and a layer of broad, greatly thickened cells. The unequal desiccation of these layers is the cause of the curving up of the lateral walls of the valves, which at last approach so near to one another as to exercise considerable pressure on the seeds in the middle. The result of this pressure is that the smooth seeds are shot out with about the same force as is imparted to a cherry-stone when it is flicked to a distance by the finger and thumb. The seeds are ejected in regular succession. The foremost seed of the first carpel goes first, and the seeds at the opposite extremity are discharged last. It is not till the first carpel is quite empty that the second begins to part with its seeds, and the third only comes into play when the second is finished. The drawing together of the two sides of the valve always begins at the free extremity of the valve, and lasts until all the seeds have been ejected.

In many Mimoseæ, Cæsalpineæ, Papilionaceæ, Sterculiaceæ, and Acanthaceæ the seeds are expelled by means of a spiral torsion of the valves of the fruit at the moment that the legume or capsule opens. The wall of the fruit of these plants includes a soft succulent layer of thin-walled parenchymatous cells, and a hard layer of strongly-thickened elongated cells, which run obliquely from one edge to the other in each valve. The rupture of the fruit, and the spiral torsion of its valves at the moment of their separation, depend upon these diagonal cells of the hard layer. Each one of these cells winds itself into a spiral as it dries, and consequently the entire layer undergoes a corresponding torsion. The tissues composed of thin-walled cells, which are in connection with the hard layer, offer no resistance to the movement, and the rotation is therefore so sudden and violent that the seeds contained in the pod are projected to a distance. If the fruit is short, the valvular torsion is confined to ½–1 twists; if long, the spiral includes 2 or even 3 complete coils, and the valves of the empty fruit are curled up like ringlets (e.g. *Lotus corniculatus*, see p. 431, fig. 325[3], and *Orobus vernus*, see fig. 459[1]). The force of projection varies according to the thickness of the hard layer. In *Castanospermum australe*, where the pod-valves attain to a thickness of 5 millimetres, the sudden torsion causes the expulsion of spherical seeds, measuring 3·5 centimetres in diameter, and weighing 16 grams. In these cases the valves of the fruit persist upon the fruit-stalks after the ejection of the seeds, and herein lies the essential difference between them and those expulsive fruits of which the carpels break away from the stalks with the seeds. To this class of expulsive fruits belong also several Papilionaceæ, such as the *Dorycnium* mentioned at the beginning of this section, and besides them the genus

Kitaibelia of the family Malvaceæ, *Alstrœmeria* amongst the Liliaceæ, several Acanthaceæ, including the *Acanthus mollis* (see figs. 459[7] and 459[8]), which Goethe has made familiar to us, the wonderful parasite, *Lathrœa clandestina*, and many Euphorbiaceæ (e.g. *Euphorbia, Hura, Hyœnanthe, Mercurialis, Ricinus*, see figs. 459[9] and 459[10]). In all these plants the fruit-valves are comparatively short, and the spiral torsion is therefore less clearly manifested. The impulse given to the seeds by the twisting of the valves is supplemented by various other contrivances which cannot here be described, and, as a matter of fact, the range of projection in this group of sling-fruits is wide as compared with that of others.

A peculiar form of sling-fruit is found in several of the Diosmaceæ, Rutaceæ, and Zygophyllaceæ. In these plants a complete separation of the hard from the soft layer takes place. When the seeds are ripe the external soft layer dries, splits along the ventral suture, and contracts strongly. In consequence of this contraction the hard internal layer, which is in the form of a case inclosing the seeds, is forced out of the slit. As soon as the hard case is thus set at liberty its two lateral walls part asunder, assume the shape of the screw of a steamer, and eject the seeds to a distance. Similar processes occur in the genus *Collomia* of the family Polemoniaceæ, but in this instance it is not the soft outer layer of the valves but the calyx, which, on drying, exercises pressure on the inclosed case, and the latter, which is extruded, is not the hard layer only but the entire dry capsule. The liberation of the case is here materially assisted by the circumstance that the three valves of the capsule disunite at a time when they are still surrounded by the calyx, and hence exert a counter-pressure upon the calyx. When once the capsule is freed from the grasp of the calyx, its valves diverge still more widely from one another and eject their seeds. In *Eschscholtzia* also the entire fruit is jerked off the receptacle, but here the phenomenon depends on the fact that the two valves of the siliquose fruit attain to a high degree of tension on desiccation and tend to curve outwards. When the tension has reached a sufficient pitch to sever the connection between the fruit-valves and the receptacle, the whole fruit is shot away from the stalk in a curve. In the Stork's-bill (*Erodium*, see vol. i. p. 619, figs. 147[3] and 147[4]), and in several Umbellifers (e.g. *Scandix*), the entire fruit is not thrown off, but the constituent parts of the fruit with their tightly inclosed seeds are jerked away from the central axis.

This cursory survey is sufficient to give an idea of the great variety existing amongst the sling type of fruit. Of course the fruits in question are always placed in such a position as to render a free flight of the seeds possible. In every case where the fruits before ejecting their seeds or being themselves jerked away are for any reason hidden under foliage-leaves, or are borne by stalks which bend downwards, as in the Wood-sorrel and the Violet (see figs. 458[3] and 458[4]), the stalks straighten out just before expulsion takes place and lift the fruits up above the leaves. In most instances the angle of projection is 45°, and, as is well known, the greatest range of flight is thus attained. The ejected seeds are spherical, oval, bean-shaped, or lenticular. In the last case they are expelled in such a manner as

to cut edgewise through the air, and it is the invariable rule for seeds to be so ejected as to encounter as slight a resistance from the air as possible whatever their shape may be. Contrivances for determining the direction in which the expelled body is to move are rare. A first indication of some such adaptation occurs in the Wood-sorrel (see fig. 458 [8]) and in *Ricinus* (see fig. 459 [10]), where the seeds are thrust through an opening of definite shape. In the Acanthaceæ (*Justicia*, *Acanthus*, &c.), the path of projection is determined by the circumstance of the seeds resting before their expulsion against rigid curved bars springing from the partition-wall which runs through the fruit (see fig. 459 [8]). The act of expulsion is usually accompanied by a characteristic noise like that of the bursting of a bladder, and the sound amounts to a regular detonation in the case of the dehiscence of the fruits of *Hura crepitans*. The range of projection is least when the seeds are small and light, and greatest when they are large and heavy, as is shown by the following table:—

Name of Plant.	Shape of Seed.	Longest Diameter of Seed in Millimetres.	Shortest Diameter of Seed in Millimetres.	Weight of Seed in Grams.	Range of Projection in Metres.
Cardamine impatiens	ellipsoidal	1·5	0·7	0·005	0·9
Viola canina	oval	1·6	1·0	0·008	1·0
Dorycnium decumbens	spherical	1·5	1·5	0·003	1·0
Geranium columbinum	spherical	2·0	2·0	0·004	1·5
Geranium palustre	cylindrical	3·0	1·5	0·005	2·5
Lupinus digitatus	cubical	7·0	7·0	0·08	7·0
Acanthus mollis	bean-shaped	14·0	10·0	0·4	9·5
Hura crepitans	lenticular	20·0	17·0	0·7	14·0
Bauhinia purpurea	lenticular	30·0	18·0	2·5	15·0

It will be noticed that as a means of distribution the agency of expulsive fruits is confined to a very restricted range. As compared with the distances to which seeds are conveyed by other means, such as the wind, the range of projection of the most powerful contrivances for expulsion, viz. 15·0 metres, is inappreciably small. This may account for the facts, firstly, that expulsive fruits are produced by comparatively few plants; and secondly, that such plants as do possess them are for the most part denizens of localities that are sheltered from the wind, where, therefore, the conditions are not favourable to dispersion by that agency. *Cardamine impatiens*, *Dentaria*, *Impatiens*, *Lathræa clandestina*, *Mercurialis perennis*, *Orobus vernus*, *Oxalis Acetosella*, *Viola canina*, and *V. sylvatica* all inhabit retired and shaded woodlands, whilst others, as, for instance, *Geranium palustre* and *Lathyrus sylvestris*, climb over bushes and hedges on the borders of woods. Mention must also be made of the fact that in many cases a second mode of dispersing fruits and seeds acts conjointly with that of expulsion, as is indicated by the name of *Impatiens Nolitangere*, *i.e.* "Touch me not". Those sling-fruits, for instance, in which the high degree of tension is due to the swelling up and turgidity of particular layers of cells, are so constructed that the slightest touch on the outside causes a relaxation of the tension and the ejection of the seeds in the direction of the object that has touched the fruit. The animals which frequent the shady woods

where *Impatiens, Cardamine, Dentaria, Oxalis,* &c., grow, brush against the fruits of those plants in the course of their wanderings, and at once receive a charge of seeds, some of which are sure to be left sticking to the creature's fur or feathers. It has long been known that when animals pass over places that are overgrown by *Elaterium* (see fig. 458[1]) and brush against its fruits, which hang down from hook-shaped stalks, they are bespattered with the mucilaginous mass in which the expelled seeds are embedded, and that as soon as they reach a place of rest they endeavour to get rid of the unpleasant encumbrance.

Several contrivances for the distribution of fruits and seeds remain to be described which, so far as regards their results, exhibit the greatest resemblance to the above sling-fruits, although the causes which determine the phenomenon in their case are utterly different. In the last-named the forcible expulsion is due to cellular turgescence, or to movements brought about by the drying up of hygroscopic cell-layers; in the cases now to be described the result depends solely on the elasticity of stems and fruit-stalks. The stems and stalks in question are strongly resilient, and are strained and curved by a force acting from without. The moment the force ceases to act, their quality of resilience causes them to return to their former position, and in doing so they jerk the fruits and seeds borne by them to a distance. Of these contrivances, which are called balistic means of dispersion of fruits and seeds owing to their analogy to catapults or balistas, we will here deal with five forms. The simplest occurs in the Compositæ, whose fruit-capitula are borne upon erect, comparatively long, elastic, flexible stems. The small fruits of the capitulum are already detached from their short pedicels by the time they are ripe and are deposited upon the central disc of the receptacle, which is surrounded by involucral scales, or at the bottom of the basket-shaped fruit-capitulum into which the floral-capitulum develops. They are so deeply bedded in this situation that it is not possible for them to fall out unless subjected to some external impetus. But the erect resilient stem which bears the capitulum has only to be bent to one side by a gust of wind or by the touch of an animal for the fruits lying on the fruit-capitulum (which is flat or excavated as the case may be) to be shot off by the recoil which ensues. In many of the Compositæ the involucral scales which form the enveloping basket bend towards one another at the top so as to constitute a roof; they are, however, elastic and flexible and very smooth on the inner surface, so that the fruits when ejected easily slip by them, and yet are to a certain extent guided in the course they take by the tips of the scales. In other Composites, of which the genus *Telekia* is an example, the floral receptacle is thickly clothed with so-called paleæ, and the fruits to be ejected, which, it may be noted incidentally, have no pappus, are embedded amongst these paleæ. The paleæ are erect and stiff, and are edged with small, upturned teeth; the slightest shock sends the fruits a little higher up amongst the scales, and they cannot then return to their former position, as the stiff marginal teeth bar the way. The fruits thus seem to make their way up the scales, step by step, as though they were ladders. If, when they have nearly reached the top, there comes a gust of wind which sets the peduncles of the capitula

rocking to and fro, the fruits are thrown out from between the elastic tips of the scales and describe an open curve before they reach the ground. A third group of Composites, which may be represented by *Centaurea Pseudophrygia* and *C. stenolepis*, exhibits the following arrangement: The receptacle is destitute of paleæ, but the involucral scales form a sort of basket at the bottom of which are the fruits. In damp weather the tips of the bract-scales close tightly together, and the short bristles of the pappus crowning each fruit are applied closely to one another. In warm, dry weather especially, under the influence of a dry wind and sunshine, the scales part asunder and the basket stands wide open. At the same time the hairs

Fig. 460.—Catapult fruits.

[1] and [2] *Salvia verticillata*. [3], [4], [5] and [6] *Teucrium Euganæum*. [7] and [8] *Teucrium flavum*. [9] *Monarda fistulosa*. [10] and [11] *Polygonum Virginicum*. [1], [3] and [10] nat. size; the others magnified.

of the pappus bristle up, and in so doing raise the fruits to the open mouth of the basket. If the peduncle supporting the capitulum is now set in motion, the fruits are tossed out like shuttle-cocks. The bristly pappus-hairs are not in this case organs of flight; they are short and stiff, and, besides raising the fruits, serve also to determine the direction of their fall. Balistic apparatus very similar to that just described is also found in several *Iridaceæ*, *Liliaceæ*, *Caryophyllaceæ*, *Primulaceæ*, and *Scrophulariaceæ*, only in them the erect, resilient stem does not bear a fruit-capitulum but a capsule, and the ejected particles are not fruits but seeds. The seeds are comparatively large and heavy, and are destitute of membranous or hairy appendages. In all these cases the capsule is situated with its orifice upwards and only opens in dry weather. As its cavity is very deep, no ejection of the seeds ensues except when the resilient stalk which carries it sways somewhat violently to and fro.

The manner in which the fruits of Labiatæ are thrown off is particularly remarkable. The fruits in question are spherical, oval, or ellipsoidal nutlets, and when ripe are still hidden at the bottom of the persistent calyx. The calyx is either bell-shaped or tubular, and faces laterally; the pedicel supporting it is resilient, and usually bowed (see figs. 460 [1, 2, 3, 6]). If one presses upon the stiff points of the calyx with some hard object such as a piece of wood (fig. 460 [5]) the pedicel is subjected to a strain, and as soon as the pressure ceases it springs back to its former position, and the nutlets are shot out with great force (fig. 460 [6]). The path of projection is in this case determined by the two inferior calyx-teeth, which curve upwards like sledge-runners (see fig. 460 [2]). In many instances, as, for example, in *Teucrium flavum*, *T. Euganæum*, and *Monarda fistulosa* (see figs. 460 [3, 4, 5, 6, 7, 8, 9]), there is yet another contrivance for ensuring the proper direction of flight. This consists in the presence of stiff though pliable convergent hairs in the calyx-tube, and their function may be compared to that of the grooves in a rifle. Again, in *Scutellaria* the lobes of the calyx-limb, which is in the form of a tilting helmet with the visor down, determine the path of the seeds after expulsion. The result thus artificially attained by bending down the stalks of the fruiting calyces and letting them fly up again is brought about in nature by gusts of wind, by drops of rain, and most frequently of all by animals brushing against the calyces. In the last-mentioned event one or other of the ejected nutlets may stick to the animal's coat and be carried to a much greater distance than would otherwise be the case. This kind of apparatus rarely occurs in plants other than Labiatæ. The nearest analogy is found in the ejection of seeds from the fruits of several species of the Chickweed genus, *e.g. Cerastium macrocarpum* (see p. 448, fig. 340 [4]), where the fruits are curved like the letter S, are borne on stiff stalks and hold the ends that open upwards.

One of the most curious forms of mechanism of the catapult variety occurs in the North American *Polygonum Virginicum* (see figs. 460 [10] and 460 [11]). In this plant the fruits are on short stalks, and are arranged in spikes on long switch-like stems. The fruit-stalks are remarkable for the fact that the cells of the cortical parenchyma, which is greatly developed, have their walls strongly lignified, though only slightly thickened. It is also noteworthy that between the stalk and the fruit there is a layer of separation which looks like a joint to the naked eye. The style is transformed into a decurved beak, which is seated upon the fruit, and terminates in two little divergent hooks. When one of these fruits is pushed by a passing animal it is at once detached at the separation-layer and springs away to a distance. The pressure applied to the fruit is apparently transmitted to the short stalk, and gives rise to a condition of tension in the tissue of the stalk analogous to that of a watch-spring. As soon as the pressure ceases the tension relaxes, and the fruit is cast away with great force. For a long time it remained a mystery how these fruits were thrown off in the absence of any animals to give the initial impulse. A few years ago, however, I succeeded in observing the manner in which the long fruiting switches are swayed backwards and forwards by a boisterous wind,

and how they brush against one another and against the branches of neighbouring shrubs as they swing, and thus receive the stimulus necessary to cause them to throw off the fruits. The contact of animals is, however, a more advantageous means of dispersion, inasmuch as the fruits may be left hanging to their coats by the hard styles and the range of distribution be greatly increased thereby. When there is no assistance from animals, and the cast-off fruits simply fall to the ground, the range of projection is not more than 2–3 metres, which is a comparatively small distance from the spot where the fruits were ripened.

The limitation of the range of dispersion is still more marked in the case of fruits which creep or hop along the ground than in those where the action is that of a sling or of a catapult. The fruits in question have stiff and very hygroscopic bristles projecting on one side from their external coats, and these bristles continually change their position according to the varying state of the environment in respect

Fig. 461.—Creeping and hopping fruits.

[1] *Ægilops ventricosa.* [2] *Ægilops ovata.* [3] *Crupina vulgaris.* [4] *Trifolium stellatum*

of moisture, and by so doing propel the fruit or seeds, as the case may be, in a definite direction. The awns which project from the glumes of Grasses (e.g. *Elymus crinitus*, *Secale fragile*, and various species of *Ægilops*; see figs. 461 [1] and 461 [2]), the strong bristles in which the bract-scales of the flowers in Restiaceæ terminate (*e.g.* the South African plant, *Hypodiscus aristatus*), the calyx-bristles and stiff pappus-hairs in Scabiouses and Composites (e.g. *Crupina vulgaris*, see fig. 461 [3]), and the divergent calyx-teeth in Papilionaceæ (e.g. *Trifolium stellatum*, see fig. 461 [4]) constitute structures whereof the different parts alternately approach and recede from one another and so cause a movement resembling that of creeping. In all these cases the hygroscopic structures are furnished with small teeth. Sometimes the teeth are on both sides, sometimes on one side, and sometimes only at the tip (see figs. 462 [1, 2, 3, 4]). The teeth render retrogression impossible, and to that extent determine the direction in which the fruit moves. In *Avena elatior*, *Avena pratensis*, and several other Grasses the awns which project from the base of the enveloping glumes are bent elbow-wise. The part below the bend is spirally twisted, and as the tissue is extraordinarily hygroscopic, the spiral relaxes or contracts according to the amount of moisture in the air. This spiral motion causes the part of the awn which is above the bend to move like the hand of a watch, but now to one side, now to the other. Of course this movement can only

take place provided the part of the awn which undergoes it is not fixed down anywhere by an obstacle. If one of the lever-arms of the awn encounters a fixed object on the ground the spiral motion of the lower arm sometimes has the effect of forcing the tip of the awn over the obstacle, so that the whole structure shoots obliquely upwards. This phenomenon is especially conspicuous in *Avena sterilis*. In this case two glumes furnished with strong bent awns are to be seen on the fruiting spikelet after it has fallen. An alteration in the environment in respect of moisture causes the two awns to twist in opposite directions, so as to cross one another. After pressing one upon the other, they ultimately slip apart with a sudden jerk, which causes the whole fruit to spring up. This movement is much more like hopping or jumping than creeping.[1]

The distance traversed by creeping, hopping, and bounding fruits is seldom greater than a few decimetres. The movements generally land the fruits almost

Fig. 462.—Fruits which creep or hop along the ground.

[1] Awn of *Ægilops ventricosa*. [2] Awn of *Ægilops ovata*. [3] Bristles of the pappus of *Crupina vulgaris*. [4] Calyx-teeth of *Trifolium stellatum*; all the figures magnified.

immediately in some *cul de sac*, where they remain, or else the awns gets entangled with the above-ground stems and leaves, and in that case the result of the movements is to imbed the seeds, which are concealed in the fruit-scales, in the earth (see vol. i. p. 617). In such cases no doubt the most important function of the movements in question is to fix the plants in the soil, but on the other hand it cannot be denied that a limited form of dispersion may be and is as a fact achieved by these movements.

The dispersion of fruits through the agency of water takes place in all plants which undergo fertilization under water and detach their fruits when they are quite ripe. To this class of fruits belong the Fungi of the family *Saprolegniaceæ*, and most of those Cryptogams which are known as Algæ. Such facts as have been ascertained by botanists concerning the distribution of the fruits of these plants in the water have been recorded in previous pages (see pp. 49 and 64). This method of dispersion is of less importance in the case of Phanerogams, which are fertilized and ripen their fruits in the medium of the air. At first sight one might

[1] The hopping movements of the fruits of the Mexican plant named *Sebastiana Pavoniana*, and of those of *Tamarix Gallica*, which belongs to the Mediterranean floral area, are not due to alterations in the tension of particular parts of the fruit-coat, but are caused by insect-larvæ which live inside the fruits. In the case of the "Mexican Jumping Bean", the larvæ are those of the small lepidopterous insect named *Carpocapsa saltitans*, and in *Tamarix Gallica* those of the beetle *Nanodes Tamarisci*.

suppose that rain-water running off the plants and then trickling along the ground would be a very effectual means of dispersing fruits and seeds, but closer observation convinces one that distribution is comparatively seldom effected in this manner, and that wherever such dispersion does occur it is invariably supplemented by some other means of dissemination. The best-known instances are afforded by two plants which, on account of their extraordinary properties, were brought to Europe from the East by pilgrims and crusaders in the Middle Ages. They were called "Roses of Jericho", and all sorts of marvellous tales were told concerning them. One of these plants is *Anastatica Hierochuntica*, a Crucifer which grows on the Steppe-lands of Egypt, Arabia, and Syria, and which has the peculiarity that its branches

Fig. 463.—Fruits which open upon being wetted with water.

[1] *Anastatica Hierochuntica*, dry. [2] The same when wetted. [3] Fruit of *Mesembryanthemum Candolleanum*, dry. [4] The same when wetted. [5] Fruit of *Mesembryanthemum annuum*, dry. [6] The same after being wetted.

curve inwards when the fruits are ripe in such a manner as to form a basket round the closed, pear-shaped siliquas, which are very numerous and are situated at the extremities of the ramifications, and to protect them from being touched (see fig. 463 [1]). The shape of the structure in this condition is something like that of an unopened rose, and it remains unaltered so long as it keeps dry. When moistened the branches at once open back and stretch straight out (see fig. 463 [2]). The fruits also open at the same time, and the seeds are then liable to be washed out of the fruit-valves by falling rain. When growing wild *Anastatica* remains closed during the long drought which follows the maturation of the fruits, and it is not till the winter rains set in that the tangle of branches opens and the seeds are washed out of the fruits. The second "Rose of Jericho", *Asteriscus pygmæus*, is a small plant of the Composite family, and ranges from the northern portion of the Sahara to Palestine, being met with in especial abundance in the neighbourhood of Jericho. In this case the branches do not close together when the fruits arrive at maturity, but the involucral leaves, which are arranged in a rosette, close up over the capitula

of fruit and do not open until the winter rains set in and cause the "rose" to unfold, whereupon the fruits are washed away.

Similar phenomena in connection with the rainfall are exhibited by the fruits and seeds of the so-called Ice-plants (*Mesembryanthemum*) which occur in a great variety of forms at the Cape. The capsular fruits of these plants remain closed in dry weather; but the moment they are moistened the valves covering the ventral sutures of the fruit-loculi open back, dehiscence takes place along the ventral sutures, and the seeds, hitherto retained in a double shroud, are washed out of the loculi by the rain (see figs. 463[3, 4, 5, 6]). Amongst plants belonging to the flora of Europe, the Yellow Stone-crop (*Sedum acre*) responds to the influence of rain in a manner which reminds one strongly of the Ice-plants above referred to. The carpels are arranged radially, and are furnished at the base with wing-like borders, whilst the central part of the external surface of the fruit is in the form of a shallow basin. In dry weather the five fruit-loculi are closed; but the moment a drop of rain falls upon the concave centre they open wide, and the next few drops wash out the seeds, which are of small size, and convey them to the ground. As the rain trickles into the tiniest crevices in rocks and walls, the seeds are carried into holes in vertical or even overhanging cliffs where it would be scarcely possible for them to be deposited by any other means of dispersion. In the case of *Veronica Cymbalaria*, which grows on walls in the south of Europe, the fruits likewise remain closed so long as the weather is dry and only open when they are thoroughly soaked. The seeds are then carried, like those of the Stone-crop, into the holes and crevices of vertical walls by means of the infiltration of rain. Similarly in the cases of *Veronica agrestis* and *Veronica serpyllifolia*, species of Speedwell which grow profusely on cultivated ground, the seeds are washed out of the gaping capsules by rain and conveyed to spots where they find conditions favourable to germination. It is worthy of note that the capsules of *Veronica Anagallis*, *V. Beccabunga*, and *V. scutellata*, species which grow on banks and in running water, also do not open until they are thoroughly wetted by rain. The explanation of this curious fact must be as follows. If the wind were to act as the means of dispersion there would be a risk of the seeds being deposited on dry places where they would be doomed to perish. On the other hand, the rain carries the seeds on to the wet soil of the marsh or into the shallow water of the brook or pond, as the case may be, where the plant in question finds favourable conditions.

I must again repeat that actual contrivances with a view to seeds being washed out of open fruits by rain are comparatively rare. This, of course, does not exclude the possibility of fruits or seeds unprovided with such contrivances being dispersed by rain, or by the little tributaries of rivulets, which result from showers of rain if once they are transferred by any means into the channels in question. The rills of water which run swiftly down to join larger streams after a violent fall of rain collect not only sand and earth, but also any seeds that may have been deposited on the ground by the wind, and they subsequently set them down with the mud at the edge of the stream. Those fruits and seeds also which fall by chance into running

water, during transportation by aërial currents, may be floated along, and finally deposited by the stream. Numbers of fruits and seeds of the most various kinds of plants are invariably found to have been deposited on the banks of sand by the sides of mountain-torrents, and on the margins of rivers and rivulets after the water has subsided from a state of flood. Many of them, it is true, have no chance of developing, but perish, either because the conditions are unfavourable, or because they have lost their capacity for germination in the transit; others do, however, germinate, and some even thrive luxuriantly. But such seeds can only be said to have been accidentally dispersed by running water, and must not be considered as instances of adaptation to that method of dispersal.

The same statement applies generally to the chance deposition of the fruits or seeds of land-plants in the sea. They may be carried away to a great distance by ocean-currents, may float about for months, and finally be stranded on some remote coast. Experiments have frequently been made with a view to ascertain which fruits and seeds retain their power of germination notwithstanding prolonged immersion in salt water. As a result of these experiments it has been established that the seeds of *Asparagus officinalis*, *Hibiscus speciosus*, and several other plants do not lose their capacity for germination after immersion in sea-water for a period exceeding a year in duration, a fact which is in itself of great interest. But such results are without significance in relation to the dispersion of fruits and seeds, unless it be also ascertained that the fruits and seeds in question keep afloat upon the surface of the water. For most fruits and seeds sink at once, and sooner or later undergo decomposition at the bottom of the sea. The number of fruits or seeds capable of keeping afloat on the surface for any length of time is extremely small. Of the fruits which are found floating on the sea we may mention first the hard-coated fruits of the group of Palms named Lepidocarynæ. They have a smooth, scaly, completely closed envelope which is impermeable to water, and looks very like a coat-of-mail, and, owing to the fact that this envelope is not in immediate contact with the fruit, but is separated from it by a layer of air, the fruits are able to float on the surface of the water. The large fruit of the Cocoa-nut Palm also is rendered buoyant by a substantial layer of fibres, which incloses a quantity of air, and is itself coated by a layer with fatty contents which prevents the infiltration of water. If fruits of this kind fall into the sea and are cast up by the waves, the seedlings inclosed in them may develop and become denizens of the shores to which they have drifted, provided the conditions, in respect of climate and soil, are such as to permit it. As a matter of fact, fruits cast up by the sea on to remote islands in the Tropics have been known to develop without any human interference.

The phenomena connected with the dispersion of fruits and seeds in still water are altogether peculiar. Currents arising from the slope of the ground do not occur in such water, whilst currents set in motion by the varying temperatures of different layers of water, for the most part, ascend and descend merely, and can occasion very little horizontal displacement of fruits and seeds. The wind is the only agency in

these circumstances that can supply the propelling force necessary to drive such fruits and seeds as can keep afloat from one shore to another. Special mention must be made of three groups of fruits and seeds belonging to this category. These are, firstly, dry fruits which are rendered buoyant by air-inclosing envelopes, as, for instance, in the case of the marsh-plants known as Sedges (*Carex ampullacea*, *C. vesicaria*, &c.), where the fruit is surrounded by an inflated utricle; secondly, the fruits of Water-Plantains, Flowering-rushes, &c. (*Alisma*, *Butomus*, *Sagittaria*, *Sparganium*, &c.), which are furnished with a thick air-filled cortical parenchyma; and, thirdly, the seeds of some Water-lilies. In the case of the white Water-lilies

464.—Dispersion of fruits and seeds by the wind.

[1] *Anthyllis Vulneraria*; two fruiting calyces are falling from the plant. [2] Longitudinal section through a fruiting calyx belonging to the same plant; the pod is visible in the interior. [3] *Trifolium tomentosum*; one head of inflated fruiting calyces is detached, and another is still attached to the stalk. [4] Longitudinal section through a fruiting calyx belonging to the same. [5] *Medicago scutellata*. [6] *Ostrya carpinifolia*; branch with two fruit-spikes. [7] Longitudinal section through the saccate cupule which envelops the nut in this plant

(*Nymphœa*), each seed is enveloped in a coat (*arillus*), which loosely clothes the outer integument (*testa*) of the seed, so as to leave a layer of air between the two. In the species of the genus *Nuphar* there is no arillus, but the carpels separate when the fruit is ripe into two layers, of which the outer one is green and succulent, whilst the inner one is white and charged with air, and incloses a large number of seeds. In all these cases the seeds are enabled to float by their envelopes, and are driven along on the surface of the water by the wind.

In a similar manner the wind causes certain detached as well as aggregated fruits to roll along upon level ground. This phenomenon is observed particularly in regions where a long period of drought follows the short summer season of development; and accordingly the plants concerned are especially abundant in the vicinity of the Mediterranean Sea and in Steppe-lands. Several Umbellifers indigenous to the high

Steppes of the East produce smooth, ellipsoidal fruits about the size of a hazel-nut and so light that if one of them is laid on a person's open hand when his eyes are shut he does not perceive its presence. The extraordinarily small weight of these fruits is due to the fact that their structure includes a layer resembling the pith of the Elder. A fruit of *Cachrys alpina* measures 13 mm. in length and 10 mm. in thickness and weighs 0·07 grm.; another *Cachrys* fruit from Shiraz is 15 mm. long and 10 mm. thick and weighs only 0·06 grm. When fruits of this kind fall they are rolled along over the Steppe by the wind and only come to rest when they are caught in some crack in the parched clay soil or get lodged in a hole in a rock. A few Papilionaceæ also produce rolling fruits of the kind. One of the groups of species belonging to the Medick genus, of which *Medicago scutellata* (see fig. 464[5]) may be taken as a type, has pods which are spirally curled into round balls and which, when their seeds are ripe, detach themselves from their stalks and are rolled

Fig. 465.—Dispersion of fruits and seeds by the wind. *Plantago Cretica.*

a little way along the ground every time there comes a gust of wind. The same thing happens in the case of *Blumenbachia Hieronymi*, a native of South America, belonging to the family Loasaceæ. Although the spherical fruit of this plant has a diameter of 2·5 cm. it only weighs 0·34 grm. when thoroughly dried. As soon as the seeds are ripe the fruit-stalk withers and the round fruits, which are then left lying loose upon the ground, are rolled away by the gentlest breeze. If their career is stopped anywhere, and they get wetted by rain, the openings which are already formed in them become enlarged and a quantity of wrinkled seeds fall out. *Paronychia Kapella* (see fig. 468[6]), a plant of wide distribution in the floral area of the Black Sea, where it grows on dry rocky soil, brings small fruits to maturity in the height of summer, each of which is surrounded by silvery white membranous bracts. When the season for the dispersion of these fruits arrives the entire tuft of fruits, which is in the form of a spherical glomerule, becomes detached from the branch on which it grows and lies lightly on the ground, where the least puff of wind imparts to it a swift rolling motion. Sometimes if the ground is uneven the rolling is converted into a hopping and springing motion, and occasionally such masses of fruit are raised by powerful gusts of wind and carried considerable distances through the air. In several species of Clover, such as *Trifolium globosum*, *T. subterraneum*, and *T. nidificum* (see fig. 468[10]) there are only a few perfectly

developed flowers in the cluster growing at the end of the flower-stalk, whilst a number of abortive flowers are crowded together in a tuft in the middle of the inflorescence. At the season when the legumes are formed from the fertile flowers the calyx-teeth of the abortive flowers increase in size and assume the shape of long hairy bristles, which bend over outwards and form a loose globular inclosure round the head of leguminous fruits. These balls afterwards become detached from the stalk and are rolled away by the wind.

Even entire plants are in some cases uprooted or have their stems severed from the roots at the base in the fruiting season, and are then rolled along like balls by the wind. The most remarkable instance is that of *Plantago Cretica*, which is shown in fig. 465. This is an annual plant possessing an abbreviated main axis from which springs a tuft of stiff, erect flowering stems. When the fruits begin to ripen the stems curve down in coils to the periphery of the plant, and by so doing give a strong pull to the abbreviated axis and to the simple tap-root, which is inserted in the earth in a vertical position. The soil on which *Plantago Cretica* grows being completely dried up in summer is full of cracks, and the pull imparted in the manner described is in consequence sufficient to uproot the plant. The plants now in the fruiting stage have the form of flattened balls and are very light, so that the entire structure is rolled along by gusts of wind. *Plantago Cretica* is also a type of the so-called "Steppe-witches" and "wind-witches", which are a source of so much wonder to travellers in the regions of Steppes. On the high table-land of Persia there is a plant named *Gundelia Tournefortii* which grows in loose, round, prickly sods, and has a tap-root deeply sunk in the earth. When the fruits are ripe the neck of the root rots away and the round sod then rests simply with its stiff lower branches in contact with the ground. Whenever the slightest wind begins to blow innumerable quantities of these sods are set in motion, and are thus dispersed over the plateau. The herbaceous plants of the Steppes of Southern Russia which exhibit the phenomenon of a decay of the bases of the stems in the fruiting season and a consequent liberation of the dry aërial portion of the plant belong to families of the most various kinds. The most common are *Alhagi camelorum*, *Centaurea diffusa*, *Phlomis herba-venti*, *Rapistrum perenne*, and *Salsola Kali*. It often happens that a number of these dry, branching herbs get hooked and entangled together as they roll along, until at length they form a ball as big as a cartload of hay. Such balls have also been seen lifted up by whirlwinds and driven bounding over the plain. It is not surprising that this marvellous phenomenon has appealed to the imagination of the inhabitants of the Steppes, and has even become a subject for witch-lore whence have arisen the names Wind-witch and Steppe-witch.

It only happens in a small proportion of these cases of rolling fruits, wind-witches, and the like, that the seeds are strewn out as they are bowled along; when this does occur it is usually occasioned by some unevenness in the ground which gives a sudden jog to the rolling body. In the majority of cases the seeds do not escape until the fruits are brought to rest by encountering some insurmountable obstacle, the reason being that the seed-vessels only open when they become wet.

This brings us back to the fruits of *Mesembryanthemum* and *Anastatica*, which were described on pp. 845, 846. Sometimes these also play the part of rolling fruits. The capsules of *Mesembrianthemum* detach themselves from their stalks, the plants of *Anastatica* become partially uprooted, and lie during the dry season of the year loose upon the earth. A puff of wind blows them into hollows in the ground or cracks in rocks, where they are held prisoners. The seed-cases, however, still remain closed. At last the winter rains set in, whereupon the capsules open, the seeds are washed out, and after a short time they germinate on the saturated ground, to which the rain has conveyed them.

Innumerable are the cases of wind-dispersed fruits and seeds which remain floating in the air for a period of more or less duration after severance from the mother-plant, and which have their fall retarded by special contrivances for the purpose. The conformation of fruits and seeds of this category must be such that the air offers great resistance to their fall, and it is important that they should possess as small a weight as possible in relation to their size. It is well known that the spores of Fungi often remain for a long time floating in the air as constituent particles of the dust. Some seeds, too, are so extraordinarily light that they also look simply like dust and are able to remain for a comparatively long period suspended in the air. Amongst such dust-like seeds those of Orchids must be mentioned first. A single seed of *Goodyera repens*, for instance, weighs only 0·000002 grm. Several other plants, particularly parasites and saprophytes which live in deep beds of humus, possess extremely light seeds, as is shown by the annexed table:—

Name of Plant.	Weight of Seed in grams.	Name of Plant.	Weight of Seed in grams.
Stanhopea oculata	0·000003	*Sempervivum acuminatum*	0·00002
Monotropa glabra	0·000003	*Parnassia palustris*	0·00003
Pyrola uniflora	0·000004	*Sedum maximum*	0·00004
Umbilicus erectus	0·000006	*Lepigonum marginatum*	0·00007
Gymnadenia conopsea	0·000008	*Spiræa Aruncus*	0·00008
Orobanche ionantha	0·00001	*Veronica aphylla*	0·0001

To enable these seeds to float in the air for as long a time as possible they are more or less flattened, and their centre of gravity is so placed that they always present the broad side to the direction of descent. The same form of adaptation occurs in seeds which are shaped like leaflets, scales, or delicate discs. A compressed seed is usually surrounded by an attenuated margin, a membranous border, or a radiating fringe of extremely fine processes, as in *Funkia, Lilium, Tulipa, Fritillaria, Rhinanthus, Veronica, Lepigonum, Cinchona, Bignonia, Dioscorea*, and *Heliosperma* (see p. 423, figs. 318 [4, 5, 7], and figs. 466 [2, 4, 5]). In some cases the entire pericarp is modified in this manner, as in *Hymenocarpus, Mattia, Peltaria, Ptelea*, and *Ulmus* (see fig. 467 [4], and p. 143, fig. 232 [2]). Amongst Umbelliferæ, Mimoseæ, Papilionaceæ, and Cruciferæ cases also occur in which the mericarps, the segments of siliculas and lomenta, or the seed-studded valves of ordinary pods and siliquas,

according to the particular plant considered, are in the form of scales and leaflets which become detached separately. Instances of this kind are afforded by *Artedia squamata*, *Megacarpæa laciniata*, *Mimosa hispidula*, *Æschynomene glabrata*, and *Lunaria rediviva* (see figs. 467 [1, 5, 11], and p. 445, fig. 339 [1], and fig. 466 [1]).

With these forms may be classed also such fruits and seeds as are furnished with wing-shaped appendages. The wings are either produced from the seed-coat, as in Pines and Firs (see p. 441, fig. 335 [5]), or else arise from the carpels. A single wing, which stands out to one side, is developed in the case of the pods of some tropical Leguminosæ (e.g. *Securida virgata* and *Centrolobium robustum*; see p. 445, fig. 339 [5]), and in the separate parts of the double fruit of the Maple and of the

Fig. 466.—Dispersion of fruits and seeds by the wind.

[1] Siliquose fruit of *Lunaria rediviva*; the two valves of the fruit have become detached; seeds are fastened to the inside of each valve. [2] Opened capsule of a *Bignonia* from which winged seeds are being carried off by the wind. [3] Capsule of *Heliosperma quadrifidum* after dehiscence; the seeds are being shaken out by the wind. [4] A seed of *Heliosperma quadrifidum* magnified. [5] Capsule of a *Dioscorea* after dehiscence, the winged seeds being blown away by the wind.

Banisterias, belonging to the Malpighiaceæ (e.g. *Acer Monspessulanum* and *Banisteria Sinemariensis*; see figs. 467 [7] and 467 [10]). The achenes of Birches and of the Tree of Heaven (e.g. *Betula verrucosa* and *Ailanthus glandulosa*; see figs. 467 [2] and 467 [12]) bear two laterally placed wings in each case. The mericarps of many Umbelliferæ (e.g. *Opoponax Cretica* and *Laserpitium latifolium*; see figs. 467 [6] and 467 [13]) have wings projecting from the back; the fruits of some Polygonums (e.g. *Polygonum dumetorum* and *P. Sieboldi*; see fig. 467 [3]) are furnished with three wings, and those of *Triopteris bifurca*, one of the Malpighiaceæ, with four wings, of which two are large and two small (fig. 467 [9]). In other cases some of the floral-leaves are transformed into wings for the fruit, as, for instance, in *Dryobalanops*, of the family Dipterocarpeæ, in which five sepals are in the form of long wings (see fig. 468 [5]), and in *Gyrocarpus*, of the family Combretaceæ, in which two of the 4–7 unequal segments of the calyx are similarly adapted (see fig. 467 [8]). It is of common occurrence for the fruits to become winged

in consequence of the continuous growth after the flower has faded and the ultimate desiccation of persistent bracts, as is seen in the Hop (*Humulus Lupulus*), the

Fig. 467.—Dispersion of fruits and seeds by the wind.

1 *Megacarpæa laciniata.* 2 *Ailanthus glandulosa.* 3 *Polygonum Sieboldi.* 4 *Ptelea trifoliata.* 5 *Æschynomene glabrata.* 6 *Opoponax Cretica.* 7 *Banisteria Sinemariensis.* 8 *Gyrocarpus Asiaticus.* 9 *Triopteris bifurca.* 10 *Acer Monspessulanum.* 11 *Artedia squamata.* 12 *Betula verrucosa.* 13 *Lasserpitium latifolium.*

Oriental Hornbeam (*Carpinus Orientalis*), and the Lime (*Tilia intermedia*) (see figs. 468[1] and 468[2]). In many cases, as, for instance, in the Tree of Heaven (*Ailan-*

thus), the two wings exhibit a slight spiral twist resembling a propeller; thi occasions a peculiar gyratory motion of the fruit as it sails along in the ai Wherever there is only a single wing which projects from one side, the centre c gravity has an eccentric position, and the fruits and seeds of this class spin quickl

Fig. 468.—Dispersion of fruits and seeds by the wind.

[1] *Carpinus Orientalis.* [2] *Tilia intermedia.* [3] *Armeria alpina.* [4] *Melica altissima.* [5] *Dryobalanops.* [6] *Paronychia Kapela.* [7] *Briza maxima.* [8] *Scabiosa graminifolia.* [9] *Humulus Lupulus.* [10] *Trifolium nidificum.*

as they fall freely through the air. The motion in question is particularly well marked in the half-fruits of the Sycamore and the seeds of Pines.

The same object as is attained in the above cases by the development of alate processes is brought about in other plants by the transformation of dry bracts or floral-leaves into light, loose, saccate, or inflated envelopes round the fruits or seeds

When quite dry, these envelopes are extremely thin and delicate, and sometimes their weight is still further reduced by a portion of the tissue being torn during desiccation, in which case the whole assumes a sieve-like or latticed appearance. The small fruit within the envelope defines the position of the centre of gravity, and consequently determines also the attitude of the structure as a whole that best adapts it to dispersion by the wind. In several Papilionaceæ, as in *Callipeltis cucullata* and the yellow-flowered species of Clover (e.g. *Trifolium agrarium* and *T. badium*; see figs. 469[1, 2, 3, 4, 5]), the dried petals of the corolla are fashioned into an envelope which incloses the small 1-seeded legume, and in several species of Lady's Fingers (e.g. *Anthyllis tetraphylla* and *A. Vulneraria*; see figs. 464[1] and 464[2]), and some species of Clover of the tribe *Vesicastrum* (e.g. *Trifolium fragiferum* and *T. tomentosum*; see figs. 464[3] and 464[4]), the inflated calyx plays the same part. In many Labiates also (e.g. *Calaminta, Salvia, Thymus*), the calyx is converted into a dry, saccate envelope, which is severed from its stalk by any external stimulus, and then serves as a means of dispersing the ripe nutlets contained in it. In the Hop-hornbeam (*Ostrya*, see figs. 464[6] and 464[7]), the small nut is enveloped in the sac-like bract; and in many Grasses, as, for instance, *Briza maxima* and *Melica altissima* (see figs. 468[4] and 468[7]), the dry glumes constitute a covering to the small fruit which adapts it to dispersion by the wind.

Fig. 469.—Dispersion of fruits and seeds by the wind.

Trifolium badium. — [1] Inflorescence. [2] Same with fruit ripened. [3] Flower. [4] Fruit enveloped in the dried petals. [5] Longitudinal section through the fruit in its envelope of petals. — *Verticordia oculata*. [6] Fruit. [7] Longitudinal section through the fruit. [8] Five "feathers" from the fruit. [3], [4], [5], and [8] magnified.

One of the commonest devices for keeping fruits and seeds suspended in the air is of the nature of a parachute. This form of mechanism occurs in the shape either of tufts of hairs or of membranous borders. In Willow-herbs (*Epilobium*; see fig. 472[6]), Asclepiadaceæ (e.g. *Cynanchum*, see fig. 471[6]), and several Bromeliaceæ

(e.g. *Tillandsia*; see fig. 475 [2]) only one pole of the seed is furnished with a tuft of hairs, whilst in *Adenium* (see fig. 471 [2]), belonging to the family Apocynaceæ, both poles are so provided. In Valerianaceæ (e.g. *Valeriana*; see fig. 471 [3]) and in Compositæ (e.g. *Senecio* and *Taraxacum*; see figs. 471 [1, 8, 9]) the tuft of hairs which acts as a parachute springs from the upper extremity of the achene. Sometimes the parachute and the body it keeps in suspension are connected by a slender stalk (e.g. in *Tillandsia* and *Taraxacum*); but usually the former is directly sessile on one extremity of the seed or indehiscent fruit as the case may be. In *Verticordia* (see figs. 469 [6, 7, 8]), of the family Myrtaceæ, a strange and beautiful parachute is formed by five petals which are in the form of little fans, each composed of ten

Fig. 470.—Dispersion of fruits and seeds by the wind.

[1] *Bombax*. [2] *Anemone sylvestris*. [3] *Gossypium Barbadense*.

feather-like lobes, and in some Labiatæ, as, for instance, *Micromeria nervosa* (see fig. 471 [7]), the radiating, hair-studded segments of the fruiting calyx constitute a similar apparatus. On the other hand, in several other Labiatæ (e.g. *Ballota acetabulosa*), in many Plumbaginaceæ (e.g. *Armeria*; see fig. 468 [3]), and in several Dipsaceæ (e.g. *Scabiosa*; see fig. 468 [8]) the parachute is developed from the delicate, dry membranous calyx or from the epicalyx. Nor must reference to the Cape Silver Tree (*Leucadendron argenteum*, one of the Proteaceæ) be omitted. The fruits here are produced in large cones not unlike those of the Stone Pine (*Pinus Pinea*) in form and dimensions. Each bract of the ripe cone subtends a fruit consisting of a nut with persistent wiry style and stigma. The 4-lobed perianth also persists as a membranous parachute, its originally free apices having become connate above the nut and around the style. Ultimately the original attachment of the perianth below the ovary becomes dissolved, and as the nut falls out of the cone

the style (with nut suspended below) slides out of the hole, around which the perianth-lobes are connate, until its further progress is arrested by the button-like

Fig. 471.—Dispersion of fruits and seeds by the wind.

[1] *Senecio vulgaris.* [2] *Adenium Honghel.* [3] *Valeriana tripteris.* [4] *Typha Schuttleworthii.* [5] *Eriophorum angustifolium.* [6] *Cynanchum fuscatum.* [7] *Micromeria nervosa.* [8] and [9] *Taraxacum officinale.* [10] *Salix Myrsinites.*

stigma. The perianth here forms a beautiful parachute, with the nut hanging freely below at the end of a string, like an enterprising balloon-gymnast.

From the fruits and seeds equipped with parachutes we pass to those which are embedded in masses of wool or in envelopes of silky hairs, and are thereby enabled

to remain poised in the air. The hairs arise either from the surface of the seed-coat (*testa*), as in the Cotton trees (*Bombax* and *Gossypium*; see figs. 470 [1] and 470 [3]), or else they spring from the base of the seed, as in Poplars and Willows (*Populus* and *Salix*; see p. 423, figs. 318 [3] and 318 [4]; p. 424, fig. 319 and fig. 471 [10]). In the Bulrush (*Typha*; see fig. 471 [4]) they take their rise from the pedicels of the fruits, and in several Ranunculaceæ (e.g. *Anemone sylvestris*; see fig. 470 [2]) from the achenes themselves. In other cases they arise from the floral-leaves, as, for instance, in the Cotton-grass (*Eriophorum*; see fig. 471 [5]), where the structure which repre-

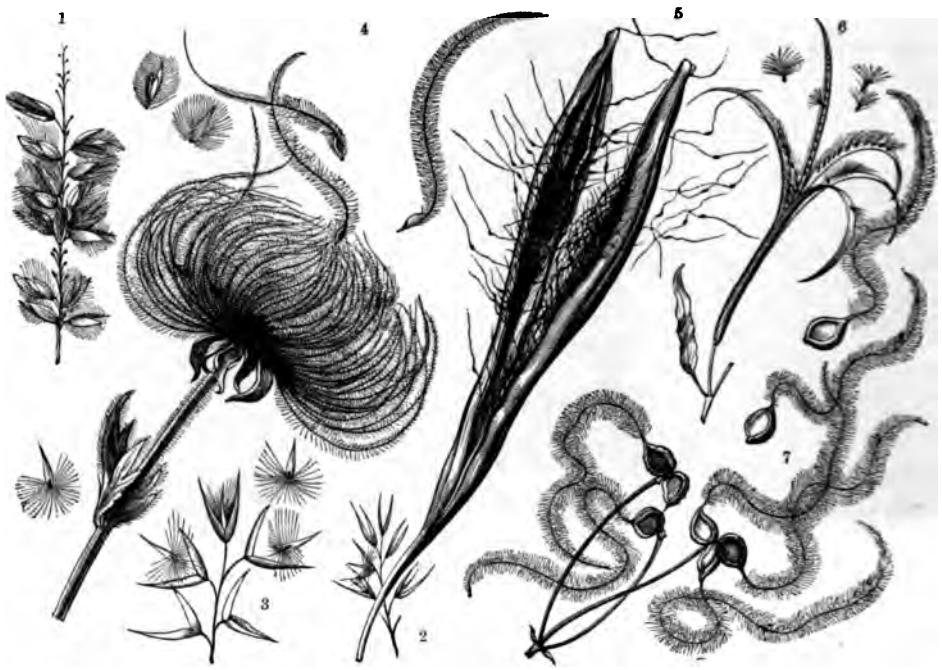


Fig. 472.—Dispersion of fruits and seeds by the wind.

[1] *Melica Balansæ.* [2] *Calamagrostis Epigeios*; nat. size. [3] The same magnified. [4] *Geum montanum.* [5] *Æschynanthus speciosus.* [6] *Epilobium collinum.* [7] *Clematis Flammula.*

sents the perianth is transformed into delicate hairs, and in *Trifolium plumosum*, where the fruiting calyx is wrapped in wool. In many Grasses the glumes are beset with extremely fine hairs (e.g. *Melica* and *Calamagrostis*; see figs. 472 [1, 2, 3]), in *Micropus*, of the Compositæ, long hairs project from the scales of the involucre and envelop the entire capitulum in a flocculent mass, and in the Venetian Sumach or Wig-plant (*Rhus Cotinus*) the stalks of abortive flowers are covered with a woolly down, which serves for the dispersion of the fruits, whose stalks are usually free from wool. Lastly, we have the cases where the fruits or seeds are kept suspended in the air for a more or less prolonged period by means of special hairy tails. Either the seeds are tailed at both ends, as in *Æschynanthus* (see fig. 472 [5]), one of the Gesneraceæ, in which the tiny seeds are furnished with two long hairs, one at each end, or else the style lengthens after the flower has faded and becomes converted into a spirally-curved tail, which remains attached to one side of the

achene, and acts like a parachute, as may be seen in *Geum*, *Atragene*, *Pulsatilla*, and *Clematis* (see figs. 472[4] and 472[7]). In some Grasses, such as *Stipa* (see vol. i. p. 619, fig. 147[1]), an awn is developed in the form of a long feather, which soars above the tightly-closed glumes inclosing the fruit.

Several of the fruits and seeds above described are directly exposed to the wind. Owing to the fact that the desiccation of the envelopes and stalks of the fruits at the time of ripening of the seeds renders certain layers of tissue brittle, a moderate wind is sufficient to cause the fall of such fruits, and the same gust that brings about their severance from the plant drives the fruit along in a horizontal direction. The fruit does not fall to the ground until the wind drops, or until its progress is arrested by some obstacle.

Many other fruits and seeds detach themselves spontaneously from the mother-plant when they are ripe, but are not directly exposed in consequence to the full shock of the wind. In these we find many contrivances for the purpose of ensuring that the parts to be dispersed shall be brought out from their shelter, and given over to the wind at the proper time. In some tropical Orchids which are epiphytic on the bark of old trees (viz. *Aerides*, *Angræcum*, *Sarcanthus*, *Saccolabium*, &c.), the capsular fruits contain, in addition to the small seeds, hair-like cells, with spirally-marked and obliquely-pitted walls (see fig. 473). *Vanda teres* (see fig. 475[1]) may be taken as a type of this group. The hair-like cells in question are woven together into a sort of felt. They are extremely hygroscopic, and twist and turn about in a curious manner if the slightest change of condition in respect of moisture occurs.

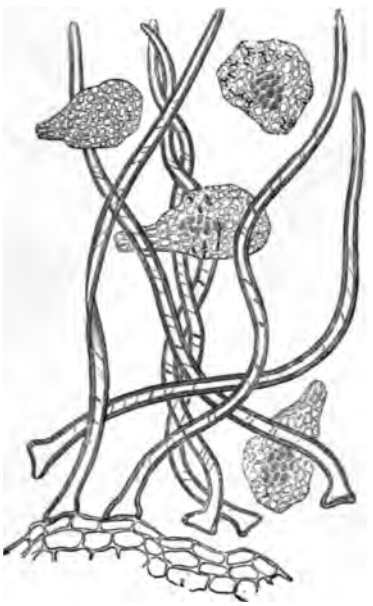


Fig. 473.—Seeds of the Orchid *Vanda teres*, which are moved from the interior to the surface of the capsule by hygroscopic hair-like cells, and are thus exposed to the wind; ×100.

When the valves of the capsules move apart under the influence of a dry wind, an active movement is simultaneously initiated in the matted hairs. The felt becomes to a certain extent puffed up, and consequently it squeezes out between the valves of the capsule, and drags the seeds, which are imbedded amongst the hairs, from the interior to the surface of the capsule, where they are liable to be blown away by the least breath of wind. This happens, as was said, when a dry wind is blowing. In wet weather the capsules close up, and conceal both hairs and seed once more in their interior. Similar phenomena may be observed in the fruit-capitula of some Composites whose fruits are spontaneously detached from the receptacle on ripening. In damp weather the loose achenes lie hidden in the involucral cup, as though at the bottom of a basket, and the hairy pappuses appended to the achenes are clubbed together. When the atmosphere is dry, the involucre, which is composed of hygroscopic scales, opens, and the pappuses of the fruits within spring apart, and so act as

levers. The fruits are speedily raised by this means above the edge of the open involucre to a sufficient height to expose them to the wind. In some other Composites, such as the Dandelion (*Taraxacum*), the fruits do not detach themselves spontaneously from the floral receptable when they are ripe. The segments of the involucre close together in wet weather, as do likewise the hairs or plumes of the pappus. In dry weather the involucre opens, whilst the feathers of the pappus diverge so as to assume the form of a parachute, and in that condition offer a comparatively large surface for the wind to act upon. A moderate gust of wind is now able to lift the fruits, with their expanded parachutes, off the receptacle and carry them away (see fig. 471[2]). If no breath of wind stirs, they remain upon the receptacle; the damp atmosphere of evening causes both parachutes and involucre

Fig. 474.—Dispersion of fruits and seeds by the wind. Fruits of a Thistle (*Cirsium nemorale*) floating in the air and becoming detached from their parachutes and dropping to the ground whenever they encounter an obstacle in the course of their flight.

to close up again, and the process of dispersion is suspended until next day, when the air is dry once more and the sun shining. In *Andropogon Ischæmum*, *Avena pratensis*, and many other Grasses, the flowering glume has an awn composed of spirally-marked and highly hygroscopic cells, and bent like an elbow, and this awn undergoes a marked spiral torsion, accompanied by a slight downward flexure whenever the air is dry. The distal arm of the awn is liable to get pressed against objects in the course of these movements, and it then acts as a lever in raising the fruits above the outer glumes. They are then easily blown away by a puff of dry wind. In several Scabiouses, also, the breaking up of the fruit-capitulum, and the raising of the fruits with a view to their dispersion by the wind, are occasioned by a bristling movement on the part of the hygroscopic setæ of the calyx. Each fruitlet in the Valerian is surmounted by a pappus of delicate feathery hairs. When the air is damp these feathers are folded together; when it is dry they become unfurled (see fig. 471[3]). In this condition of divergence, they present an ample surface to the wind, and the slightest gust detaches the fruits and blows them away. A similar phenomenon occurs in *Dryas*, and in some other plants; but we cannot now enter into the details of these cases.

In the case of Willow-herbs (*Epilobium*) and of some Pines (*Pinus nigricans*, *P. sylvestris*, &c.) the fruit-valves and fruit-scales which cover the seeds only open back under the influence of the sun's warmth, and when a dry wind is blowing, and the same wind which thus operates on the valves and scales also carries off the seeds the moment they are exposed, they being furnished with wings or tufts of hair with a view to aërial dispersion. The reader must be referred to p. 447 for a description of the manifold effects of a dry wind on the fruits and seeds in question. First, the dry capsules open; secondly, the seeds, hitherto lying in the interior of the fruits, where they are protected against moisture, are shaken out by the swaying to and fro of the elastic fruit-stalks; and thirdly, these seeds are caught up and scattered by the wind.

The distance to which fruits and seeds which are adapted to aërial transit by means of wings, hairy tails, parachutes, inflated envelopes or woolly coverings, as the case may be, are conveyed by the wind depends on the degree of perfection of their mechanism, on the condition of the air in respect of moisture, and on the strength of the current of air by which they are transported. When the weather is calm and sunny, innumerable of the lighter fruits and seeds are carried up to a great height by the ascending currents which are generated in the atmosphere; but they usually descend again after sunset at a little distance from the spot where they were taken up. Such excursions do not conduce so much to a dispersion of plants over large areas as to their deposition on shelves and in crevices of steep walls of rock, where seeds would not otherwise easily acquire a footing. Currents moving in a horizontal direction may, it is true, convey their freight of fruits and seeds over extensive tracts of country, but very exaggerated notions are usually entertained concerning the distances thus attained. Amongst the numerous species of fruits and seeds blown by storms of wind to the tops of the Alps and left upon the snowfields above the glaciers, not a single one derived from distant parts (*i.e.* from another district) has been found after careful examination of the deposited matter; and from this we may infer that, even on mountains, fruits and seeds are scarcely conveyed any further by a raging wind than when they are blown from one side of a valley to the other.

In many plants the wings or parachutes, as the case may be, only remain attached to the seeds or fruits for the period of their journey through the air. If the winged seed of a Pine gets stranded anywhere the membranous wing drops off, and the seed is then no longer capable of flight. This phenomenon is even more marked in the fruits of Thistles (e.g. *Carduus* and *Cirsium*; see fig. 474). The achenes, which are comparatively large, are supported by parachutes and float quietly in the air, but the moment one of them strikes against any obstacle the fruit severs itself from the parachute and falls to the ground. There can be little doubt that to this mode of dispersion must be attributed the common occurrence of Thistles at the foot of walls and in hedgerows, inasmuch as the floating fruits are carried against such structures with especial frequency. In other cases the fruit or seed maintains permanently a firm connection with the parachute, and the latter

serves to fasten it to some place where the conditions requisite for germination are present. For instance, when the seeds of *Tillandsia* (see 475 [2]) come into contact with the boughs of old trees, as they are blown along in a horizontal direction, they fasten on to the bark where they are able to germinate immediately. Thus the pappus to which the seed owes its buoyancy serves subsequently to anchor it to a substratum favourable to its development.

The modes of dispersion of fruits and seeds through the agency of animals are

Fig. 475.—Dispersion of fruits and seeds by the wind.

[1] Capsule of *Vanda teres*, from which the seeds have been transferred to the air by means of hygroscopic hairs, and are being blown away. [2] Open capsule of a *Tillandsia*; the seeds are being lifted out by the wind by means of their parachutes. If a seed is blown against the bark of a tree it is anchored there by the hairs of the parachute.

almost as varied as the different methods of dissemination by the wind. In many cases such dispersion is brought about by the animals using the fruits and seeds in question for food; the undigested parts are excreted, and any embryos which may have survived the passage through the alimentary canal subsequently germinate. As the fact of this mode of dispersion has been a matter of dispute amongst botanists, and could only be established by experiment, I determined to feed various animals with selected fruits and seeds, and to ascertain first of all whether the embryos preserve their vitality after passing through an animal's intestinal canal. Fruits and seeds belonging to 250 different species of plants were used for the purpose, and

the following birds were fed with them: blackbird, song-thrush, rock-thrush, robin, jackdaw, raven, nutcracker, siskin, goldfinch, serin-finch, titmouse, bullfinch, cross-bill, pigeon, fowl, turkey, and duck; and also the following mammals: marmot, horse, ox, and pig. After each meal the fæces were examined, to ascertain what seeds they contained, and were then laid on a separate bed of earth, and at the same time fruits and seeds of the same plants which had not been used for food were planted in an adjoining bed. It would be out of place to set forth here all the precautions which it was necessary to take in conducting these laborious researches, and I shall confine myself to a statement of the most important results obtained from 520 separate experiments.

As regards the mammals subjected to experiment very few words will suffice. Almost all the fruits and seeds administered to them, whether they took them voluntarily or unawares mixed with their ordinary food, were destroyed either at once or upon being chewed with the cud. It is true that a few millet-seeds germinated from the ox-dung, and must therefore have escaped being crushed during rumination, and that one or two solitary specimens of lentil-seeds and oat-fruits similarly passed uninjured through a horse, whilst *Cornus alba*, *Hippophae rhamnoides*, *Ligustrum vulgare*, *Malva crispa*, *Rhaphanus sativus*, and *Robinia Pseudacacia* all germinated after passing through a pig; but the number of the seedlings so obtained was scarcely appreciable as compared with the number of fertile seeds swallowed in the animals' food, and the fruits and seeds of about 60 other species of plants completely lost all power of germination during their passage through the intestines. The birds resolve themselves into three groups in relation to the matter in question. The first group includes those which grind up even the hardest fruits and seeds in their muscular and hard-coated "gastric mills" which are in addition usually filled with small stones and sand. Amongst these, some strip the fruits and seeds when they first lay hold of them, and thereby condemn them to destruction. To this group the following birds of those employed in the experiments belong, viz. the turkey, the hen, the pigeon, the cross-bill, the bullfinch, the goldfinch, the siskin, the serin-finch, the nutcracker, the titmouse, and the duck. No seed capable of germination was found under ordinary conditions in the excrements of these birds; only when on a few occasions food was forcibly administered to the hen and to ducks, so that their crops must have been overloaded, were a few seeds found to have escaped pulverization, and still to possess the power of development. The seeds in question belonged to *Arenaria serpyllifolia*, *Papaver Rhœas*, *Sisymbrium Sophia*, *Ribes rubrum*, *Ligustrum vulgare*, *Fragaria Indica*, and other species. Ravens and jackdaws form a second group, in that the stones of the drupes and hard-coated seeds of the berries which they ate passed uninjured through the intestine, whilst soft-coated seeds and fruits were all destroyed. It is worth mentioning in particular that after these birds had been fed with cherries their excrements contained cherry-stones 15 mm. in diamater, every one of which was able to germinate. Of the birds selected for experiment, the blackbird, the song-thrush, the rock-thrush, and the robin belonged to a third group. Of these the

blackbird was the least fastidious about its food. It even swallowed the fruits of the Yew without afterwards relieving its crop of the stony seeds, and it never rejected a single fruit that was mixed with its food. The song-thrush refused all dry fruits of 5 mm. diameter or more, even when they were mixed with the finely-chopped meat with which the bird was fed. They also avoided certain strong-smelling fruits, such as that of the Yarrow. On the other hand, the aromatic fruits of Umbelliferæ (e.g. *Bupleurum rotundifolium* and *Carum Carvi*) were eaten with great avidity. The seeds of the Tobacco-plant, Henbane, and Foxglove mixed with the food were not rejected and caused no ill effects, and no more did the berries of the Deadly Nightshade, which were devoured greedily. On the other hand, a song-thrush sickened after eating berries of *Phytolacca*. When fleshy fruits with seeds of diameter exceeding 5 mm., such as those of *Berberis*, *Ligustrum*, *Opuntia*, and *Viburnum* were introduced into the crop, the pulp passed thence into the gizzard, but all the seeds were thrown up. Many seeds, as, for example, those of *Lychnis flos-Jovis*, were carefully removed from the rest of the food with which they had been mixed. The seeds of fleshy fruits which were greedily devoured were thrown out of the crop if the stones which they inclosed measured as much as 3 mm. The interval of time between ingestion and evacuation was surprisingly short in the birds of the third group. A thrush fed with *Ribes petræum* at 8 o'clock in the morning excreted numbers of the seeds after the lapse of three quarters of an hour, and seeds of *Sambucus nigra* were found to have passed through the alimentary canal in half an hour. The majority of seeds took from 1½ to 3 hours to perform the journey. Curiously enough, the small smooth fruits of *Myosotis sylvatica* and *Panicum diffusum* were retained for the longest period. Of the fruits and seeds which passed through the intestine of one or other of these birds, 75 per cent germinated in the case of the blackbird, 85 per cent in the case of the thrush, 88 per cent in the case of the rock-thrush, and 80 per cent in the case of the robin. The germination of fruits and seeds that had undergone ingestion and excretion was usually (*i.e.* in from 74 to 79 per cent of the cases) tardy as compared with that of similar fruits and seeds which had not been treated in this way but were only germinated for the purpose of comparison. Only in the case of a few berries (e.g. *Berberis*, *Ribes*, *Lonicera*) was the period of germination hastened. The seeds of such plants as grow on richly-manured soil (e.g. *Amaranthus*, *Polygonum*, *Urtica*) after passing uninjured through a bird's intestine produced stronger seedlings than did those which were cultivated without such advantages.

From these experiments it is evident that the dispersion of edible fruits through the agency of thrushes and blackbirds is not, as was formerly supposed, an exceptional phenomenon obtaining in the Mistletoe only, but one that may take place in the case of many other plants, and other observations prove that, as a matter of fact, it does take place. Plants possessing fleshy fruits are undoubtedly often disseminated in this manner. The occurrence of such plants as epiphytes upon trees, and also their unexpected appearance on the tops of high rocks and old walls thus receives a natural explanation.

The phenomenon in question also enables us to interpret the meaning of the changes undergone by fleshy fruits at the season when their dispersion becomes desirable, inasmuch as they serve the purpose of attracting animals, and the same consideration applies to the contrivances whereby animals are discouraged from taking the fruits before they are ripe. Mention has already been made of these latter contrivances on p. 444; and as regards the attraction of animals with a view to the dispersion of ripe fruits the following particulars are of especial interest: Fruits and seeds that are still unripe are hidden amongst the leaves of the mother-plant, have a green colour resembling that of the foliage, and are destitute of scent. On ripening the fruits are exposed, the coats of the fruits acquire a conspicuous coloration, and frequently emit a strong scent. In the cases where the seeds alone are dispersed and the pericarps are left behind, as, for instance, in *Pœonia Russi*, *Euonymus verrucosus* and *Magnolia grandiflora*, the capsules or follicles burst open, and the seeds are of a bright red or yellow colour, sometimes flecked with steel-blue and black, which renders them visible from afar. In the above-named species of *Euonymus* and *Magnolia* they emerge from the pericarps and hang at the ends of threads which renders them even more conspicuous. The particular colour assumed by fruits and seeds at the time of maturity varies according to that of the foliage by which they are surrounded. The different tones of red stand out best from a green environment; therefore, for plants with evergreen foliage (e.g. *Ardisia*, *Gaulteria*, *Ilex*, *Taxus*, *Arbutus Unedo*, *Arctostaphylos uva-ursi*, *Vaccinium Vitis-Idæa*) a red coloration is the most advantageous. Also in the case of plants with foliage which, although not evergreen, does not acquire an autumnal tint at the season when the fruits are ripe, *e.g.* the Strawberry, the Raspberry, the Currant, the Wild Cherry, and the Red-berried Elder (*Sambucus Ebulus*) the red hue of the fruits is of great value. On the other hand, red fruits would stand out but little against a background of foliage that had already donned the red or yellow tints of autumn by the time they ripened, and accordingly the fruits of *Ampelopsis hederacea*, *Cornus sanguinea*, *Prunus Padus*, *Arctostaphylos alpina*, *Vaccinium Myrtillus* and *V. uliginosum*, &c., are, as a fact, blue or black. Sometimes the fruits are black and the fruit-stalks red, as in *Sambucus nigra*, or the fruits are only coloured on the side exposed to view, as in the Apple and the Pear. The fruits of the Quince and the Pine-apple are set off by their yellow colour from the blue-green foliage. White berries, such as those of *Cornus alba* and *Symphoricarpus*, occur principally in plants which cast their leaves before the fruit is ripe. Standing out against the brown or gray background formed by the leafless branches and the fallen leaves of late autumn these white fruits are clearly visible. The extent to which fruits are advertised by their scents is a matter of common experience, and we need only refer for illustration to the Strawberry, the Raspberry, the Quince, and the Pine-apple.

Seeing that the seeds and stones containing seeds of the fleshy fruits eaten by thrushes and blackbirds only remain a short time in the crop and intestine of the bird, it is probable that the plants in question are disseminated by this agency to

the distance of a few leagues at most, in the course of a single year, and that it takes many years to distribute them, step by step, as it were, over large areas. We may reasonably suppose that distribution is effected principally in the direction of those parts of the world towards which thrushes and blackbirds are in the habit of journeying by short daily stages when autumn, the season of the maturity of most fleshy fruits, sets in.

It is well known that nutcrackers, jays, squirrels, and marmots, keep stores of food in larders, which they fit up in holes in rocks or in the earth or in some other secret hiding-place of the kind, and that such fruits and seeds as they conceal there are liable to be left permanently for one reason or another. The hiding-place may be forgotten, or, as is still more likely, the creature that occupied it may fall a victim to a bird of prey. The fruits and seeds may then germinate in the place of concealment, and, inasmuch as the latter is always more or less distant from the spot whence the fruits were taken, this must also be accounted one of the modes of dispersion of the plants in question. I have myself observed this curious phenomenon also in the case of the dissemination of the Arolla Pine (*Pinus Cembra*) by nutcrackers, of Beeches, Oaks, and Hazels by jays, and of Hazels by squirrels.

The subject of the dispersion of seeds by insects may be most conveniently dealt with in this connection. Otto Kuntze observed how ants fasten on to the pulp which surrounds the seeds of *Carica Papaya*, and push the seeds before them in companies of three, and Lundström narrates that the seeds of the Cow-wheat (*Melampyrum*), after they fall out, are carried off to ant-hills. These statements early directed my attention to the subject of the dispersion of seeds by ants, and I found that the phenomenon occurs on a very large scale. The ant *Tetramorium cæspitum*, in particular, is indefatigably engaged throughout the summer in dragging seeds to the ant-hill and storing them up there. Other species, which live in holes in the earth, hollow trees, and such places (*Lasius niger*, *Formica rufibarbis*, &c.), exhibit this form of activity, but they are much more fastidious than *Tetramorium*. Many kinds of seed, which are at once pounced upon by the last-named if they are scattered in the path of those insects, are left untouched by other species. So far as my observations go, it is the seeds with smooth external coats, but with large micropylar and hilar caruncles (see p. 425) which are conveyed to the holes, as, for instance, those of *Asarum Europæum* and *A. Canadense*, *Chelidonium majus*, *Cyclamen Europæum*, *Galanthus nivalis*, *Möhringia muscosa*, *Sanguinaria Canadensis*, *Viola Austriaca* and *V. odorata*, *Vinca herbacea* and *V. minor*, and various species of the genus *Euphorbia*. The *Tetramorium* showed a preference for the seeds of *Sanguinaria Canadensis*, which possess a very conspicuous hilar caruncle. These seeds being comparatively large and heavy, three or four small ants join forces when one is to be transferred to a hole. There can be no doubt that the caruncle, affording as it does an easily accessible supply of food, constitutes the source of attraction to the ants, and induces them to carry off those particular seeds. Neither the smooth coats of the seeds nor their contents are touched by the ants. Only thus can we interpret the fact that the seeds

dragged by ants under the ground, or into crevices in walls, germinate in those situations in the following year. It sometimes happens also that here and there a seed is left behind on the route of the ants, and in that case the caruncle is usually eaten off. Such abandoned seeds may germinate in the following year, and this explains the fact that the routes traversed by ants are regularly planted with certain species of plants. For example, in the Botanic Gardens at Vienna, the presence of *Chelidonium majus* is a constant feature of the ant-runs.

The transport of fruits and seeds to spots more or less remote from the localities where the mother-plants grow, by animals which have a definite purpose in view in so conveying them from one place to another, is on the whole a rare means of dissemination, and is confined to comparatively few species. But the unintentional dispersion of fruits and seeds by animals is of much more common occurrence. The objects thus dispersed get stuck or hooked, or otherwise fastened to animals in the course of their wanderings, and sooner or later are thrown or shaken off as being an unpleasant encumbrance. The places where such fruits and seeds are deposited are, however, always more or less distant from the spot where they ripened, and, as a general rule, they afford favourable conditions for germination.

The adhesion of fruits and seeds to the feathers of birds and to the skin or fur of other animals is due either to the agency of water, mud, and moist earth, or to that of special sticky substances secreted by the plants. In the case of many aquatic and marsh plants, such as the genera *Alisma*, *Butomus*, *Carex*, *Myriophyllum*, *Phellandrium*, *Polygonum*, *Potamogeton*, *Sagittaria*, and *Sparganium*, the fruits and seeds are unprovided either with special organs of attachment or with viscid secretions, but as was mentioned on p. 847 they have the power of keeping afloat on the surface of the water. If one dips one's hand into a pond covered with floating fruits of this kind, and draws it out again quickly, a number of the fruits always adhere to the skin by means of drops of water. The same thing happens when water-fowl rise from the water after swimming about for a time. The beak, legs, and feathers of a bird that has been shot not infrequently have the fruits in question clinging to them after the water has run off. If the bird had settled upon another pond the fruits would no doubt have been transferred to it. Adhesion through the intervention of water is assuredly by no means an insignificant factor in the dispersion of fruits to moderate distances.

The agency of mud and wet, boggy earth in affixing objects to animals is especially efficacious in the case of the numerous small fruits and seeds, which are by this means caused to adhere to birds when they come to the water's edge to drink. Jackdaws, herons, and snipe are not very particular about cleanliness, and they are invariably found to be smeared with mud. Swallows, particularly the rough-footed species, are very important members of this category, as during their sojourn on the banks of rivers and ponds they get bespattered with particles of mud. It is true that they try to cleanse themselves from all such foreign matter, but when the season for migration approaches they become restless and excited and forget the morning toilet which, until then, is performed with great care. In the same manner

water-fowl when they migrate neglect their usual habit of assiduously removing all traces of dirt, and we know from the investigations made by Darwin how great is the number of seeds imbedded in the mud. From 6¼ ounces of mud 537 plants germinated. In my own case the examinations of the mud obtained from the beaks, feet, and feathers of swallows, snipe, wagtails, and jackdaws resulted in about half as productive a yield of fertile seeds; but that is a sufficiently striking result; and when it is remembered that pigeons and cranes traverse from 60 to 70 kilometres in an hour, whilst swallows and peregrine falcons cover as much as 180 kilometres, it is clear that fruits and seeds affixed to these birds may be carried in a very short time over several degrees of latitude. The number of species of plants which are dispersed in this manner is, it is true, but small. For the most part they are water-side and of these chiefly small annual species, as is evident from the following list of those whose fruits and seeds I found most frequently in the mud taken from birds:

Centunculus minimus.	*Heleocharis acicularis.*	*Lythrum Salicaria.*
Cyperus flavescens.	*Isolepis setacea.*	*Nasturtium amphibium.*
„ *fuscus.*	*Juncus bufonius.*	„ *palustre.*
Elatine Hydropiper.	„ *compressus.*	„ *sylvestre.*
Erythræa pulchella.	„ *lamprocarpus.*	*Samolus Valerandi.*
Glaux maritima.	*Limosella aquatica.*	*Scirpus maritimus.*
Glyceria fluitans.	*Lindernia pyxidaria.*	*Veronica Anagallis.*

Most of these species are distributed over all parts of the world, but they seldom remain for a long time in any particular locality. They often start up quite unexpectedly at places where migrating birds have rested and gone to drink. The extraordinary occurrence on the edges of ponds in Southern Bohemia of the tiny *Coleanthus subtilis*, which is indigenous to India, and the sudden appearance of the same species of grass in the West of France about twenty years ago may be unhesitatingly attributed to the mode of dispersion in question, as may also the occurrence of the tropical *Scirpus atropurpureus* on the shores of the Lake of Geneva and that of the Southern native *Anagallis tenella* on the shores of the Schwarzsee at Kitzbühel in North Tyrol.

The instrumentality of rain-soaked earth on steppes, on ploughed fields, and on roads in sticking numbers of fruits and seeds to animals' feet, whether the latter be in the form of hoofs, claws, or toes, or to their hair or feathers, as the case may be, has been the subject of repeated investigation. In the hardened earth taken from the feet of birds Darwin found a large number of seeds, of which many germinated. Many weeds which grow on fields and roadsides (*Prunella vulgaris, Malva rotundifolia, Potentilla anserina, P. reptans, P. supina, Ranunculus sardous,* &c.) depend mainly on this mode of dispersion. According to an informant, the suckers of the Gecko (a kind of lizard adapted to running about on smooth rocks and walls) are sometimes beset with fine seeds, and there can be no doubt that certain plants may be disseminated by such means over steep declivities of rock.

The excretion of sticky substances by fruits and seeds themselves must naturally

promote their becoming attached to animals. Although the adhesive materials mentioned in vol. i. on p. 615 as exuding from the fruits and seeds of various Composites, Crucifers, Labiates, and Polygonaceæ when they are wetted may be primarily devoted to fixing those structures to a substratum where they can germinate, they also frequently serve a second purpose in sticking them to passing animals. The best instance of this is afforded by the Meadow Saffron (*Colchicum*), whose seeds stick to the feet of cows, sheep, and horses by means of a comparatively large caruncle, which becomes viscid when it is wetted; in this manner the seeds are conveyed from one pasture to another. There is also an instance that has come under my own observation of a small owl (*Athene noctua*), which, in catching mice, brushed against Wormwood bushes (*Artemisia*), and when it flew away was all besmeared with the fruits, which had been rendered sticky by a previous shower of rain. The succulent berries of *Bryonia*, *Lycium*, *Solanum*, and various other Cucurbitaceæ and Solanaceæ burst on the slightest touch when they are over-ripe, and sometimes their seeds stick to the hairs and bristles of passing animals, and it seems not improbable, from the reports of travellers, that the fleshy Rafflesias, which are found principally on the routes frequented by large pachyderms, are disseminated in the same manner. The mode of dispersion of the seeds of *Nuphar* and *Nymphæa* is also very curious. Their dissemination by aqueous currents has been already dealt with on p. 848, but they are besides conveyed from pond to pond by water-fowl. In order to obtain the nutritious seeds these birds break open the fruits of Water-lilies with their bills, and in so doing are almost sure to leave some of the seeds, which are imbedded in a slimy mass, sticking to the feathers surrounding their bills. If they are suddenly disturbed at their meal they have not time to clean their bills before flying away, and so they carry the seeds with them, and do not rub them off till they reach another pond.

The fruits and seeds of several plants attach themselves to any animals that happen to brush against them by means of special glandular hairs or stalked glands. These latter consist of round cells or groups of cells which are borne on stalk-like structures springing from the epidermis, and which produce on their surfaces viscid, slimy, and resinous substances (see figs. 476 [2] and 476 [5]). The most diverse parts may be clothed with stalked glands. In *Boerhavia*, *Adenocarpus*, and *Pisonia* (see fig. 476 [4]), it is the pericarp; in *Salvia glutinosa* (fig. 476 [1]), and the various species of the genus *Plumbago*, such as *Plumbago Capensis* (fig. 476 [3]), it is the calyx; and in *Linnæa borealis* (figs. 476 [6] and 476 [7]) it is a pair of bracts closely adherent to the fruit that is beset with stalked glands. In all these plants an absciss-layer is formed in the tissue of the fruit-stalk, and as soon as adhesion takes place the fruit is severed from the plant at the region of this separating or absciss-layer. Many plants—as, for example, the annual *Cerastium glutinosum*—have glandular hairs all over them, and when the seeds are ripe and the plants partially withered and only loosely rooted in the ground, a touch is sufficient to cause leaves, stems, and fruits to stick to the hair or feathers of any animal that may happen to pass. We may add that, in the case of every plant above referred to for illustration, the

phenomenon in question is not merely a matter of conjecture, but has come actually under observation.

About 10 per cent of all Flowering Plants possess fruits or seeds which are dispersed by means of clawed or barbed processes. This mode of dissemination is very like that whereby sticky fruits attain the same object. The part of the plant which is provided with these structures hooks on to the hairs, bristles, or feathers of any bird or other animal that happens to come into contact with it. The consequence is that it is torn away and carried off by the animal. This act of depredation is of course not intentional on the part of the creature that performs it; on the contrary, such appendages are a source of discomfort, and are got rid of as soon as

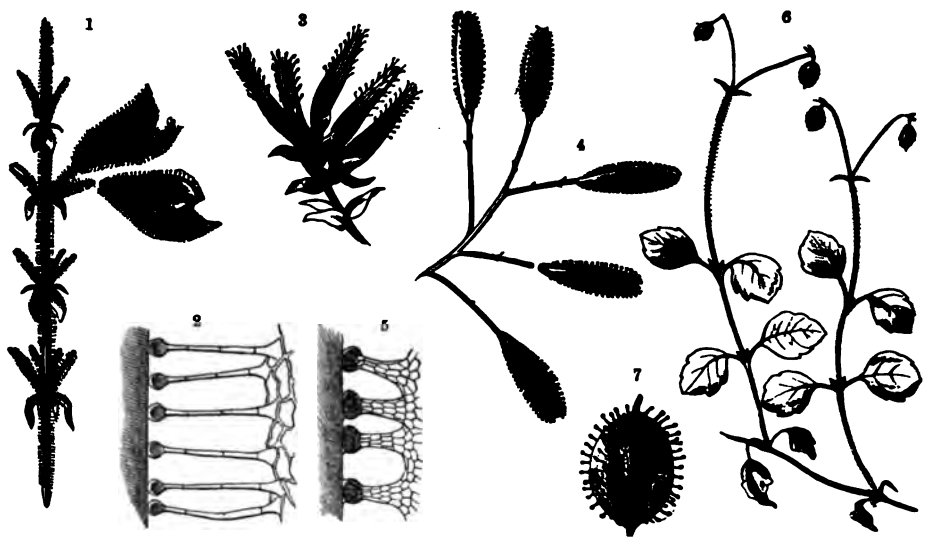


Fig. 476.—Sticky fruits.

[1] *Salvia glutinosa.* [2] Stalked adhesive glands on the fruiting calyx of the same; ×60. [3] *Plumbago Capensis.* [4] *Psoralea aculeata.* [5] Stalked adhesive glands on the fruit of the same; ×60. [6] *Linnæa borealis.* [7] Fruit of the same; ×5.

possible. But in many cases this is not accomplished until a considerable distance has been traversed, and sometimes the troublesome objects remain for weeks in the creature's coat or mane. The organs of attachment are either hooked at the tip or beset with barbs (see figs. 477 [2] and 477 [18]). In the latter case the barbs are borne on special rigid bristles or needles, and are either collected together at the top, as in a harpoon, or else are arranged in longitudinal rows as in a hackle for combing flax. Only in a few instances (*e.g.* in *Polygala glochidiata*, *Stellaria glochidiata*, and *Limnanthemum nymphæoides*) do these structures, which may be classed together as hooked bristles and hooked prickles, occur on the seeds themselves; usually they are appendages of the pericarp, and as such exhibit every degree of size possible, from the delicate, hooked bristles on the small nutlets of the Enchanter's Nightshade (*Circæa*, see figs. 477 [8] and 477 [9]) to the thick, firm claws on the fruits of the African Harpoon Fruit (*Harpagophytum procumbens*). The hooked spines of the latter fruits attain to the size of crows' feet, and are a notorious source of vexation to

ruminant animals, both wild and tame. In the Transvaal and on the Orange River the spring-boks sometimes tread upon them unawares, and when that happens the sharp claws grasp the hoof and the animal is driven to frenzy by the pain and gallops madly away, but is unable to set itself free from the instrument of torture. It is often several days before the capsule breaks up and falls off. The fruits, which

Fig. 477.—Fruits furnished with hooks.

[1] *Galium Aparine.* [2] Hooked bristles of the fruit of the same. [3] *Hedysarum Canadense.* [4] A piece of the lomentum of the same. [5] Hooked bristles of *Hedysarum Canadense.* [6] *Cynoglossum pictum.* [7] Hooked prickles on the fruits of the same. [8] *Circæa Lutetiana.* [9] Hooked bristles on the fruit of the same. [10] *Torilis Anthriscus.* [11] Single fruit of *Torilis Anthriscus.* [12] Curved prickles on this fruit. [13] *Lappago racemosa.* [14] Single fruiting spike of the same. [15] *Setaria verticillata.* [16] Fruit-bearing branchlet with involucral bristles from a spike of *Setaria verticillata.* [17] *Bidens bipinnata.* [18] Single fruit of the same. [19] Fruit of *Caccinia strigosa.* [20] Hooked prickles on the fruit of *Caccinia strigosa.* 2, 4, 5, 7, 9, 11, 13, 14, 16, 18 and 20 magnified.

are armed with hooked bristles or prickles, are so numerous that even a superficial account of them cannot be undertaken here, and we must content ourselves with mentioning a few of the most remarkable forms. Amongst these are the capsular fruits of *Krameria Ixina* and *Triumfetta Plumieri* (see figs. 478[10] and 478[11]), the sheathed achenes of several species of *Calligonum* and *Rumex*, e.g. *Rumex nepalensis* (fig. 478[3]), the pods of many Papilionaceæ (e.g. *Medicago agrestis* and *M. radiata*, *Onobrychis æquidentata* and *Hedysarum Canadense*; see figs. 478[2] and 478[9], and

figs. 477 [3, 4, 5]), the nutlets of several Boraginaceæ (e.g. *Echinospermum*, *Cynoglossum*, and *Caccinia*; see figs. 477 [6, 7, 19, 20]), the several segments of the lomenta of *Æschynomene patula*, the jointed siliquas of *Tauscheria lasiocarpa*, the schizocarps of some species of the genera *Asperula* and *Galium* (e.g. *Galium Aparine*; see figs. 477 [1] and 477 [2]), and the mericarps of many Umbelliferæ (*Caucalis*, *Daucus*, *Orlaya*, *Sanicula*, *Torilis*; see figs. 477 [10, 11, 12], and figs. 478 [6]). Other contrivances exist, but are much rarer. Such are the bending of the sepals, when the fruit is ripe, so as to convert the calyx into a claw, as in the genus *Rochelia* (see fig. 478 [8]), the assumption by the teeth of the fruiting calyx of the form of hooked prickles, as in *Valerianella echinata* and *V. hamata*, *Trifolium spumosum*, *Ballota rupestris*, and *Marrubium vulgare* (see fig. 478 [1]), the presence on the achenes of Composites of 1, 2, 3, or 4 hooked prickles in the place of a feathery pappus, as in *Bidens bipinnata* (see figs. 477 [17] and 477 [18]), the barbed character of some perianth-bristles, as in *Scirpus lacustris*, and the crowning of the hypanthium (expanded receptacle) with hooked prickles, as in *Agrimonia* (see fig. 478 [5]). As instances of the transformation of involucral leaves into hooked bristles or prickles, we may mention *Xanthium* and *Lappa* (see figs. 478 [13] and 478 [17]); whilst *Oryza clandestina*, *Paspalum tenue*, and *Lappago racemosa* (see figs. 477 [13] and 477 [14]) may be taken as representatives of the Grasses whose glumes are furnished with similar appendages.

Sometimes the entire fruit has the appearance of a claw, or is armed with large barbs, by means of which it attaches itself to passing animals. This form of adaptation is especially striking in the pods of *Krameria triandra*, *Ornithopus*, *Biserrula*, *Coronilla scorpioides*, and *Scorpiurus sulcata* (see fig. 478 [4]). The achenes of several Composites (e.g. *Rhagadiolus stellatus* and *Koelpinea linearis*) are claw-shaped, and *Koelpinea linearis* is provided in addition with a crown of sharp, curved barbs at the free extremity of each limb of the claw. In several species of the genus *Geum*, of which *Geum urbanum* will serve as an example (see figs. 478 [15] and 478 [16]), the terminal portion of the segmented style breaks off when the fruit is ripe, and the remaining part becomes converted into a hooked spine which attaches itself to any object that happens to touch it. Similarly, hooked structures are developed from the styles of several Ranunculaceæ and Pedaliaceæ. Of the latter the most noteworthy are the fruits of Martynias (*Martynia lutea*, *M. proboscoidea*, &c.), which detach themselves from the herbaceous stem when the fruit is ripe—the stem being by that time in a decaying condition—and lie loose upon the ground. Two long curved clasps, with sharp hooked ends somewhat like the horns of a chamois in form, are developed from the styles, and by means of these the fruits cling to the feet of animals which tread on them. Indeed the whole family Pedaliaceæ is of interest on account of its multifariously hooked fruits. In addition to *Martynia* the already mentioned *Harpagophytum* belongs here, and several other genera, including a Chinese aquatic, *Trapella sinensis*. In this plant the fruit is provided with 3 long appendages wound up like watch-springs, which must readily hitch themselves on to the legs of aquatic birds—or possibly even to Fishes—and in addition 2 shorter, sharp, stiff spines, which no doubt preserve the fruits against

being eaten. *Rogeria* and *Pedalium*, mentioned on p. 875, also belong to this family.

In other plants it is the fruit-stalk instead of the style which is transformed into a claw-like structure. In *Cyclamen Europæum*, for instance, the fruit-stalk undergoes spiral torsion and contraction. Formerly it was supposed that the object of this curious phenomenon was to draw the fruits into the earth, where the seeds would be favourably situated for germination. But this idea does not correspond to actual fact. The green capsules are drawn underground in the late autumn

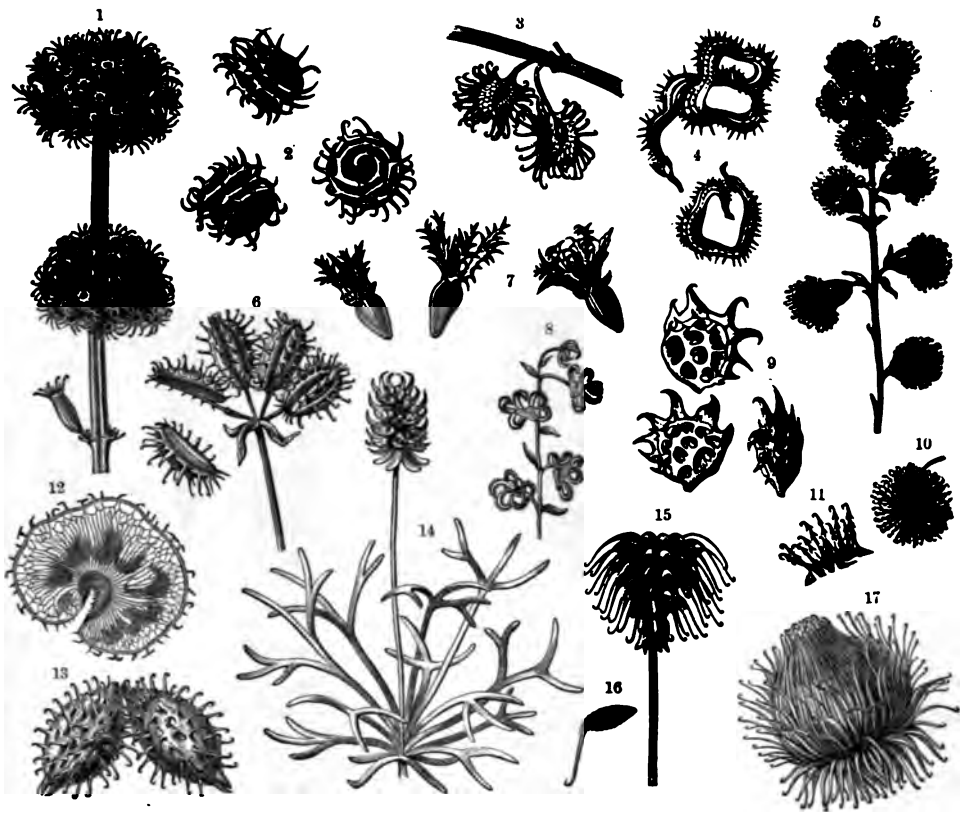


Fig. 478.—Fruits with hooks.

[1] *Marrubium vulgare.* [2] *Medicago agrestis.* [3] *Rumex nepalensis.* [4] *Scorpiurus sulcata.* [5] *Agrimonia odorata.* [6] *Oriaya grandiflora.* [7] *Pteranthus echinatus.* [8] *Rochelia Persica.* [9] *Onobrychis aquidentata.* [10] *Triumfetta Plumieri.* [11] Hooked bristles on the fruit of *Triumfetta Plumieri* magnified. [12] *Medicago radiata.* [13] *Xanthium spinosum.* [14] *Ceratocephalus falcatus.* [15] *Geum urbanum.* [16] A single fallen fruit of *Geum urbanum.* [17] *Lappa major.*

when the seeds are still unripe. They pass the winter in the earth, and do not attain to complete maturity until the following summer. The desiccation and severance of the twisted fruit-stalk then has the effect of pulling the fruit out of the ground again, the lower portion of the stalk rots, and the part which is left forms a claw surmounting the capsule. The latter, which is still full of seeds, lies loose on the ground, and adheres to the foot of any animal that treads on it. The manner in which these seeds are besides dispersed by ants has already been referred to on p. 866.

With this curious form of fruit we may associate those in which the claws or hooked prickles are metamorphosed branches, or parts of abortive flowers situated on special ramifications. It will be sufficient to adduce two examples of this group, viz., *Pupalia atropurpurea*, of the family Amaranthaceæ, and *Pteranthus echinatus* (see fig. 478[7]) of the family Paronychiaceæ. In *Pupalia atropurpurea* short branchlets spring from the axils of the bracts; a few of them bear fruits, whilst the majority are modified into hooked prickles and form a tuft which easily fastens on to foreign bodies, and becomes detached from the main axis. *Pteranthus echinatus* has several short branchlets in each inflorescence situated close to the fruit, and bearing at their extremities abortive flowers with hooked sepals.

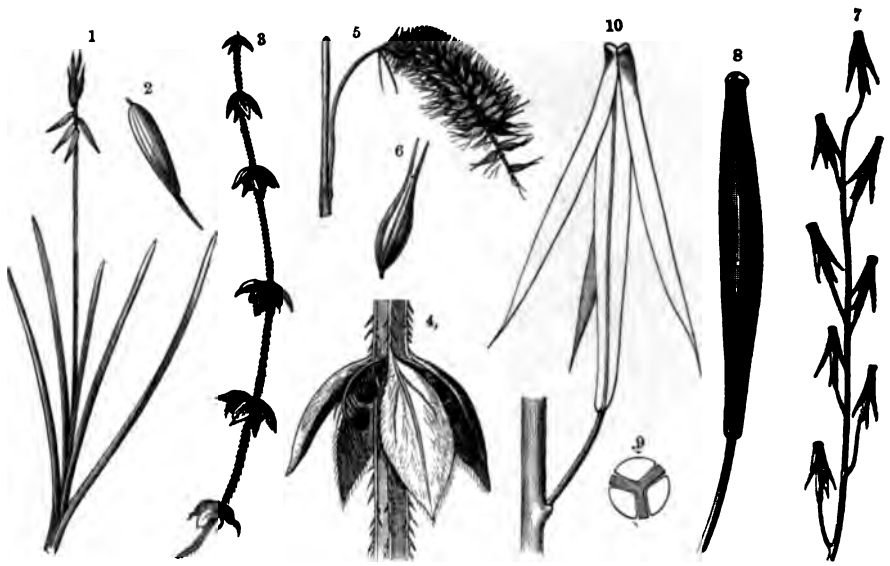


Fig. 479.—Fruits which hook on to or stick into passing objects.

[1] *Carex microglochin*. [2] Single fruit of the same. [3] *Galium retrorsum*. [4] A piece of the stem of the same. [5] *Carex Pseudocyperus*. [6] Single fruit of the same. [7] *Triglochin palustre*. [8] Single unripe fruit of the same. [9] Transverse section through the same fruit. [10] Single ripe fruit with its component valves separated. [2], [4], [6], [8], [9] and [10] magnified.

All the clawed or prickly fruits and clusters of fruit above enumerated easily come away from the mother-plant when pulled by the objects to which they have attached themselves. But there are other cases where the hooks and claws are firmly attached to the axis of the plant as a whole, so much so indeed that if the object to which they are fastened gives a pull a large piece of the stem is torn away, and sometimes even the entire plant is uprooted and carried bodily away. To this class belong the fruits of several Rubiaceæ, of which *Galium retrorsum* (see figs. 479[3] and 479[4]) may be taken as a type. The fruit-bearing stem of this plant is at once broken off or uprooted when its barbed bristles catch in the coat of a passing animal. The species of the genus *Uncaria* also are examples of the kind. The long, creeping stems develop here and there clusters of fruit and at other spots abortive peduncles, which are metamorphosed into strong, sharp claws. When these claws get hooked to an animal's foot, a more or less large piece of the stem is torn away, and with it

the fruits developed upon it. Again, in *Specularia falcata, Valerianella echinata, Cornucopia cucullata,* and *Ceratocephalus falcatus* (see fig. 478 [14]) the fruits do not sever themselves from the stems when their claws become attached to animals, but the entire plant is uprooted and carried away. A similar phenomenon is observed when a fruiting plant of *Setaria verticillata* is touched by one of the larger birds or some other animal. The fruits of this Grass are wrapped in awnless glumes and surrounded by involucral bristles furnished with very sharp barbs (see figs. 477 [15] and 477 [16]). When the bristles get fastened to an animal, not only the fruiting spike, but often a piece of the haulm as well, is dragged away, and sometimes the entire plant is uprooted and taken off. Such fortuitous appendages are very troublesome to the animal, and are got rid of as soon as possible. In many instances this is achieved without great difficulty by rubbing the coat against fixed objects, or by using the feet, snout, or beak, as the case may be, to disembarrass the body. Sometimes, however, the sharp claws and barbs of the fruits are so firmly imbedded

Fig. 480. – Fruits with needle-like spines.

[1] *Pedalium Murex.* [2] *Tribulus orientalis.*

or entangled in the hair or feathers that their extrication is attended with much difficulty and suffering.

A mode of fruit-dispersion involving still greater pain to animals is that which is accomplished by means of straight, smooth prickles projecting from the fruit, and so situated as either to bore into the foot of any animal that treads upon it, or to stick into the coat of one that merely brushes by. Two groups of these fruits may be distinguished. The first group comprises those which lie loose upon the ground when they are ripe. To it belong *Acicarpha, Ceratocarpus, Salsola,* and *Spinacia,* in which the tips of the fruiting calyx harden and are transformed into spines standing straight up, and also *Rogeria, Pedalium,* and *Tribulus* (see figs. 480 [1] and 480 [2]), in which the spines project from the fruit-walls. One of the species of the last-named genus, viz., *Tribulus orientalis,* is of common occurrence in the lowlands of Hungary, and is an object of dread to the shepherds of that region. The fallen segments into which the fruit resolves itself are armed with hard, sharp, comparatively long spines, and are often so covered with drifted sand that only the tips of the spines project above the surface (see fig. 480 [2]). These prickles pierce deep into the hoofs and soles of animals that tread upon them, and are broken off the fruit by the efforts of the latter to rid themselves of the impediment. They are thus left sticking in the skin, and cause very painful, festering wounds. As examples of the second group of fruits furnished with sharp prickles as instruments of dissemination we

may take those of *Carex pauciflora* and *Triglochin palustre* (see figs. 479 [1, 2, 7, 8, 9, 10]) These fruits are borne on a stiff, erect axis, and when ripe are pointed obliquely downwards. They easily become detached from their stalks and are left sticking like needles in the skin or fur of animals that touch them.

Straight or slightly curved bristles and prickles may take part in another way in the dispersion of fruits. When they are set in rows like the teeth of a comb on the surface of a fruit or stand out in pairs from it, as, for instance, in *Carex Pseudocyperus* (see figs. 479 [5] and 479 [6]), the woolly hairs and delicate feathers of some animals are liable to get entangled in them, and they are then dragged from their stalks. The same thing happens where the prickly processes projecting from the fruit cross one another, as in *Pterococcus*, *Sycios*, and many species of the Medick genus (e.g. *Medicago ciliaris*, *M. littoralis*, *M. sphærocarpa*, *M. tentaculata*, and *M. tribuloides*), and where the surface of the fruit or of the fruiting calyx is covered with stiff bristles forming acute angles with it, as in *Asperugo*, *Myosotis*, *Parietaria*, *Physocaulis*, and *Torilis* (see figs. 477 [10, 11, 12]). In many Grasses the awns which project from the backs of the glumes act as instruments for catching the hair of animals as they pass, and the latter is also liable to get caught between the nut and the hardened perianth-segments which surround it in several Chenopodiaceæ. It is not necessary for this that the bristles, prickles, or awns should be pointed, but it is advantageous for their surfaces to be rough or jagged, as in *Torilis* (see fig. 477 [12]). We must not omit to mention also that the tufts of hair which clothe some fruits and seeds, and act as parachutes and wings, often get entangled in the hair or feathers of animals, and thus play an additional part in dissemination. The rough coats of sheep, goats, oxen, and horses are always found to have such hairy fruits and seeds affixed to them after they have passed over ground on which herbaceous Composites, shrubby Willows, &c., grow at the season when those plants are in fruit. I have myself removed from the coats of animals of the above-mentioned kinds fruits and seeds of *Anemone sylvestris* and of various species of the genera *Calamagrostis*, *Crepis*, *Cynanchum*, *Epilobium*, *Eriophorum*, *Lactuca*, *Lagœcia*, *Micropus*, *Populus*, *Salix*, *Senecio*, *Sonchus*, and *Typha*.

Anyone who has forced his way through a thicket of poplars and willows in early summer or through a clearing overgrown by *Calamagrostis*, *Epilobium*, and *Senecio* in late summer can bear witness to the manner in which fruits and seeds of the sort in question adhere to the clothes. Sticky and hooked fruits are also found upon one after such excursions, and it is perhaps not superfluous to remark that what has been said concerning the dispersion of seeds by animals must be taken to apply also to dissemination by men. Of course we are here referring to *unintentional* dissemination by human agency. We are here concerned with the cultivation of corn, vegetables, garden-flowers, edible fruits, forest-trees, &c.—*i.e.* with the purposeful dispersion of plants by men—in so far as many of the species in question establish themselves beyond the limits of the fields or gardens, where they have been sown or planted by man, through the operation of their natural means of dissemination and without human assistance, and further, inasmuch as weeds are often

introduced into the soil unawares with the seeds of other plants, and so grow in places where they would scarcely ever obtain a footing without the interference of mankind.

Looking back over this chapter we are struck by the following points:—In the first place, the commonest contrivances and adaptations are those which confer some other benefit in addition to that of dispersing fruits and seeds. The kind of structure most often encountered in this connection serves first as a means of protecting the flowers against unbidden guests of the animal kingdom and against injurious climatic conditions, subsequently as a means of scattering the fruits, and lastly, is instrumental in attaching them to a substratum and in promoting germination. Moreover, it appears from what has been said concerning pappuses and tufts of hair, that it is no rare thing for contrivances to be adapted equally well to the dispersion of fruits and seeds by the wind, by water, or by animals. It is also of great moment to observe that most, and perhaps all, Phanerograms exhibit two methods of disseminating their fruits and seeds, one of which is adapted to considerable distances, whilst the other is confined to the immediate vicinity of the mother-plant. The former may and does, as a fact, take place on a vast scale, but it depends upon the circumstances of the environment over which the plant itself has no control. It may, therefore, in some circumstances, be completely suppressed; in other words, dispersion to a great distance may take place but does not necessarily take place. Just as the best-made machine stands still unless its wheels are set in motion by an impulse from without, so the development of the most perfect flying apparatus is of no avail if there is an entire absence of wind at the time when the winged fruit is ripe; nor do the strongest hooks serve as means of dispersion if no animals come upon the scene. On the other hand, dissemination within short distances of the mother-plant always takes place if wider dispersion fails. Supposing the fruits of a Maple-tree, when ripe, are not blown far away by a strong gust of wind, they are ultimately detached spontaneously, and drop with a gyratory motion to the ground close by the tree which produced them. Again, in the case of the Squirting Cucumber, should the expulsion of the seeds from a fruit be caused by the touch of an animal, and the seeds stick to the latter's coat, they may be carried to a distance of many miles, but if no animal happens to pass the spot where the Cucumber is growing at the time when the seeds are ripe the latter are spontaneously ejected, and the dispersion so effected does not exceed a few paces in distance. In the event of the fruits of *Cyclamen* (see p. 873), which are borne on twisted claw-shaped stalks, not being carried away by animals, they remain lying on the ground in immediate proximity to the mother-plant and the seeds germinate in that situation.

These examples, to which might be added many others, show that the same law governs the contrivances adapted to the dispersion of fruits and seeds as was found to apply to the pollination of stigmas (see p. 390). Every species of plant exhibits some mechanism designed to bring about a cross with another species, or, at any rate, with another individual. If such mechanism is unsuccessful, other

contrivances are brought into play, the aim of which is to accomplish autogamy. The open flowers of *Viola sepincola* are adapted to cross-pollination through the agency of bees; should no cross take place, and no fruits be produced from the open flowers which bloom above the ground, cleistogamous flowers, hidden underground, develop and bring forth a number of fertile seeds as a result of the autogamy which inevitably takes place within their closed floral envelopes. *Viola sepincola* may also be taken as a type of those plants in which the fruits ripen underground and produce seeds which germinate at the spot where they were formed. Such plants have always been a source of wonder to botanists, and their number is not large. The best-known examples are *Arachis hypogœa, Cardamine chenopodiifolia, Linaria Cymbalaria, Phrynium micans, Trifolium subterraneum*, and *Vicia amphicarpa*. If these plants were only to bring fruits to maturity underground, or were to draw all their fruits below the ground as soon as the seeds were mature, in order that germination and the development of new plants might ensue at that spot, their behaviour would imply a renunciation of dispersion to any distance, and the phenomenon would be highly enigmatic. The puzzle is, however, satisfactorily solved when we take into account the fact that all these plants invariably have the chance of being dispersed to great distances either before the fruits become concealed in the earth, or by means of a second form of fruit which ripens above ground, and is evidently adapted to being scattered abroad through the agency of animals, or by means of aërial or aqueous currents.

LIMITS OF DISTRIBUTION.

The results of careful computations of the numbers of seeds produced yearly by a few selected plants show that on an average a plant of *Sisymbrium Sophia* yields 730,000, one of *Nicotiana Tabacum* 360,000, one of *Erigeron Canadense* 120,000, one of *Capsella Bursa-pastoris* 64,000, one of *Plantago major* 14,000, one of *Raphanus Raphanistrum* 12,000, and one of *Hyoscyamus niger* 10,000. Each of these seeds may give rise in the following year to a new plant, which, in its turn, may produce a corresponding number of seeds. Accordingly, if a Henbane-plant developed 10,000 seeds in one year, and 10,000 plants sprang from those seeds next year, and themselves produced 10,000 seeds each, by the end of five years ten thousand billions of Henbane-plants would have come into existence. Now, as the entire area of the dry land on the earth is approximately one hundred and thirty-six billion of square metres, and there is room for about 73 Henbane-plants on one square metre, if all the seeds referred to in our hypothesis ripened, the whole of the dry land would, at the end of five years, be covered with the plants in question. In the case of *Sisymbrium Sophia*, the normal multiplication, if unchecked, would, in the course of three years, cover an area 2000 times as great as the surface of the dry land with plants.

Any such exclusive occupation of the entire earth by one or a few species is prevented by a variety of causes. As regards land-plants, the sea, separating one

country from another, constitutes an important barrier to unrestricted distribution. Even narrow straits form an insuperable obstacle to any mode of dispersion which proceeds step by step, whilst broad seas also interfere with the dissemination *per saltum*, which is accomplished by roving animals and by currents of air and water. The number of species capable of being transported across the sea by birds is so small, that the dispersion of plants as a whole is not appreciably affected by this process. The same remark applies to dissemination by water. It is well known that fruits and seeds of American plants are occasionally conveyed to Europe by the Gulf Stream, and Linnæus tells us how the seeds of the West Indian Filbert (*Entada Gingolobium*) germinated after being stranded on the coast of Norway. There is no need to point out that tropical plants of the kind would not be able to establish themselves permanently in Western Europe were it only for the nature of the climate. But even amongst other American plants to which the climate would be no drawback, not a single species is known to have come to Europe by water without human intervention. Nor has any fruit or seed achieved the crossing of the ocean to Europe through the medium of the air. America possesses a large number of Willows, Composites, and Onagraceæ of her own, which have their fruits and seeds exquisitely adapted to aërial flight, and are themselves well fitted to thrive under the climatic conditions of Europe. Nevertheless not a single instance is recorded of such a plant migrating from America to Europe through the agency of the wind. The Compositæ and Onagraceæ, which have become naturalized in Europe since America was discovered (e.g. *Erigeron Canadense, Galinsoga parviflora, Solidago Canadensis, Stenactis bellidiflora, Œnothera biennis*, &c.), were introduced in other ways, and would neither have established themselves nor have been disseminated in Europe without human intervention.

The fact that a considerable number of American plants have found a home in Europe through the agency of man alone, and independently of the movements of birds or currents, is of great interest in connection with the present subject, inasmuch as it shows that the limits of distribution imposed by the sea are only temporary, that is to say, they are only maintained so long as the present distribution of land and water remains unaltered. If Europe and America were to become connected by a bridge of land, the possibility would arise of a gradual or sudden migration across the bridge, and such plants as have been conveyed from America to Europe by human agency would be able to immigrate without such assistance, and to disseminate themselves over Europe. The external conditions would offer no impediment to their naturalization in Central Europe any more than they now do to the installation of the same species when introduced by man. As the sea limits the distribution of land-plants, so the dry land restricts the dispersion of marine plants. The larger the expanse of land between two seas, the more difficult is it for the plants which inhabit them to exchange their homes. But here again the barrier is merely temporary; for were the land to sink in any part so as to become submerged, and the two seas thus become confluent, there would be nothing to prevent the plants living in them from passing from one to the other.

The nature of the soil may constitute an insuperable obstacle to a permanent occupation of a particular district by plants, and so act as a check to dispersion. Everywhere localities with sandy, loamy, or rocky subsoils alternate with loose, wet, and porous argillaceous earths. And yet how utterly different are the conditions under which plants growing on these two kinds of soil respectively must exist. Let us consider the case of a particular species, whose seeds are uniformly scattered over a district which includes areas with different kinds of soil. In the parts where the ground possesses the requisite properties for the maintenance of the species in question, the seedlings are able to establish a firm footing, whilst those seeds which fall on uncongenial soil perish. If millions of fertile seeds belonging to a marsh-denizen were scattered over a dry tract of land, not a trace of them would be found at the end of a twelvemonth. The extent to which the chemical in addition to the physical properties of the soil operate, in producing this result, and the part played by competition between different plants for possession of the ground, have been already dealt with (p. 495 *et seq.*). From these observations it is obvious also that the distribution of species, even within a district of restricted area, is materially influenced by the soil, and that the spots in such a district where a particular species thrives and multiplies are divided from one another by tracts where it does not exist. Those restricted sites in a locality, which offer favourable conditions to the progress of a particular species, and allow of its posterity maintaining possession of the soil, where, indeed, the species is permanently established are called the habitats of that species. The botanists of former times distinguished such habitats into a large number of different classes, from which we may select the following as the most important: fresh-water springs (*fontes*), salt springs (*salina*), brooks (*amnes*), torrents (*torrentes*), rivers (*fluvii*), pools (*stagna*), lakes (*lacus*), the sea (*mare*), shores of rivers and lakes (*ripæ*), sea-coasts (*littora*), marshes (*uliginosa*), swamps which dry up in the summer (*paludes*), peat-bogs (*turfosa*), places that are periodically flooded (*inundata*), pastures (*campi*), steppes (*pascua*), deserts (*deserta*), sunny hills (*colles*), stony places (*lapidosa*), rocky places (*rupestria*), sands (*arena*), argillaceous soil (*argilla*), loam (*lutum*), débris (*ruderata*). Sufficient has been said to prove the fact that these habitats undergo various displacements, and are sometimes entirely lost, in consequence of changes effected in the soil in course of time through the action of running water and aërial denudation, or in consequence of the accumulation of humus.

The most potent influence affecting the dissemination and distribution of plants is that exercised by climate. The length of the days and corresponding duration of the sun's illumination, the temperature of air, ground, and water at the different seasons of the year, the condition of the atmosphere in respect of moisture, the quantity of water deposited by the atmosphere, and the times at which such deposition occurs in each year, the strength and direction of prevailing winds—not only are all these circumstances in general of the greatest moment to plant life, but each climatic factor stands in a definite relation to each species. If the fruits or brood-bodies of a plant are carried by any of the usual agencies of dispersion to a place

where the soil is favourable, but where the intensity of light, of warmth, or of moisture exceeds or falls short of the right measure for that particular species, the development of the species is arrested at the outset, and the plants die without leaving any offspring behind them. In this manner an absolute barrier is opposed by climatic conditions to the dispersion of each species. It must be added that the check may be given in one direction by one factor and in another direction by another climatic factor, and that not infrequently many conditions, collectively classed under the name of climate, exercise a simultaneous influence on the distribution of species.

The limits to the range of plants towards the Arctic and Antarctic regions and towards the summits of high mountains are imposed by the diminution of temperature and the increasing length of the winter, whilst the opposite boundary is encountered where the duration of daylight is still too short at the time of year when the temperature begins to be sufficient to cause the plants in question to sprout. The continental climate, which is distinguished by slight degrees of moisture, high summer temperatures, and low winter temperatures, checks those plants which suffer from dryness in summer or which cannot endure the cold of winter. On the other hand, in the case of species whose transpiration is unduly checked by a high degree of atmospheric moisture and which require an elevated temperature in summer in order to bring their seeds to maturity, bounds are set to dispersion by the climate of the sea-coast where comparatively slight variations of temperature occur during the year and where the summers are cool and the air damp. Meteorologists show us on special charts the distribution of the climatic factors by connecting all places having the same mean winter temperature, the same mean summer temperature, the same mean annual deposition of moisture from the atmosphere, and so forth, by lines which are termed isocheimal, isotheral, and lines of like mean annual rainfall respectively. The distribution of plants, in so far as it depends on climatic conditions, may be shown in the same manner by drawing lines connecting all the places at which any species is checked by climatic conditions. Such lines are called lines of vegetation, and when they run along the slopes of a mountain they coincide with the contour-lines. As each species of plant is checked in its progress towards the different quarters of the compass by different factors of climate, lines of vegetation may be drawn corresponding to the limits of range for each species to the north, north-east, east, south-east, south, &c. When all these vegetation-lines of a species are connected we obtain a curve which returns upon itself and is called a line of distribution. In most cases this line resembles an ellipse with the longer axis lying in the direction of the parallels of latitude. It is, however, not infrequently modified by influence of the nearest lines of sea-coast. The proximity of mountains also may cause variations which are principally of the nature of sinuses or bulgings.

The line of distribution incloses therefore the entire area of distribution in which the species in question finds suitable conditions and in which as a fact it grows and multiplies. Emphasis must be laid on the latter circumstance, because experience has shown that a plant-species does not necessarily grow in all the places where the conditions are favourable to its existence. Only the boundary-lines of the area of

distribution are dependent at the present day on climatic conditions; the manner in which the species has come to occupy that area has not been determined by the existing climate, but by geological processes which have always been the cause of the migrations of plants on a large scale. It also becomes a question in each individual case to what extent under past and present conditions the means of plant-dispersion would have free play.

The different areas of distribution vary greatly in size. Many species are only encountered on a single mountain, or in a particular valley, or on one island, as the case may be. These are called endemic species. As examples of such endemic species from the regions of Southern and Central Europe we may mention the following: *Iberis Gibraltarica* (Gibraltar), *Euzomodendron Burgœanum* (Central Spain), *Dioscorea Pyrenaica* (Central and Eastern Pyrenees), *Saxifraga florulenta* (Liguria and Piedmont), *Saponaria lutea* (South-western Alps), *Heracleum alpinum* (the Jura), *Hieracium Grisebachii* (the Oetzthal in the Central Alps of Tyrol), *Daphne petræa* (Val Vestino), *Rhizobotrya alpina* (Fassa and Belluno), *Gentiana Frölichii* (Carniola and Carinthia), *Wulfenia Carinthiaca* (Carinthia), *Sempervivum Pittonii* (Serpentine mountains in Upper Styria), *Schiverekia Podolica* (Podolia), *Viscaria nivalis* (Rodna Gebirge, in Northern Transylvania), *Pedicularis limnogena* (Bihar Mountains), *Hepatica Transsylvanica* (Southern Transylvania), *Haberlea Rhodopensis* (Rhodope Mountains in Roumelia), *Jankœa Heldreichii* (Thessalian Olympus), *Helichrysum virgineum* (Mount Athos), *Campanula Aizoon* (Mount Parnassus), *Hypericum fragile* (Eubœa), *Globularia stygia* (Mount Khelmos), *Genista Melia* (Melos), *Cephalanthera cucullata* (Crete), *Centaurea crassifolia* (Malta), *Petagnia saniculifolia* (Sicily), *Lereschia Thomasii* (Calabria), *Batatas sinuata* (Ischia), *Helichrysum frigidum* (Mountains of Corsica).

The species contrasting with the endemic as regards distribution, *i.e.* those whose range extends over almost the whole of the plant-inhabited earth, are called cosmopolitan. Their number is very small.

Only in the case of endemic species occupying an extremely restricted area do we sometimes find the plants evenly distributed over the whole area. They are more usually scattered unequally over the district in question. The spots where they grow in large numbers close together are separated by tracts where they do not grow at all, but where other species have taken possession of the soil, and the line of distribution then incloses separate habitats which are often at a considerable distance from each other. In such cases we speak of the area of distribution as sporadic. How far this depends on properties of the soil has been explained on pp. 495–500, and we need here only add that in mountainous or hilly countries the degree and direction of the inclination of the ground may have an important influence. Owing to the fact that a slope receives very different amounts of light and heat according as it faces north or south, different parts of a single mountain may exhibit diversities in respect of temperature and moisture as great as exist on flat ground between places separated by a degree of latitude. Also the differences in meteorological conditions between slopes facing east and west respectively, and

particularly those with south-east and south-west aspects, are much greater than is commonly supposed, and species are known, for example, which in a particular district invariably have their habitats on south-east slopes, whilst others occur only on slopes facing south-west.

It has been stated that the geological phenomena, and the changes of climate connected therewith, have at all epochs exercised an important influence on the migrations of plants, and have consequently had much to do with the displacements that have occurred in the lines of distribution. If a change occurs which results in the climatic conditions of 48° north latitude becoming such as previously prevailed at 46° north latitude, those species of plants whose range extended northwards as far as 46° proceed to take possession of suitable habitats beyond that limit and the northern line of vegetation of those particular species is sooner or later shifted northwards. On the other hand, the species which had up to that time enjoyed favourable conditions at 48° north latitude, but can no longer flourish under the new conditions, establish themselves on more suitable habitats lying further north, so that their southern line of vegetation undergoes displacement northwards. The eastern and western lines of vegetation may also be shifted in accordance with such alterations of climate as occur when an inland locality is converted into a maritime site or *vice versa*. These displacements may assume the aspect of a progression or of a retrogression, but in every instance the abandonment of the area of settlement will take the form of a migration of the plant-species concerned.

These migrations of plants which are accomplished independently of human influence take place as slowly or as quickly as the changes of climate to which they are due. In the case of species only capable of flourishing on particular habitats colonization must naturally proceed by leaps and bounds, whilst retrogression also cannot possibly take place uniformly.

The numerous habitats occupied by a species within the limits of its area of distribution are scarcely ever exactly alike in respect of the conditions which influence plant-life. Some habitats are pre-eminent on account of their advantageous position. The species in question develops most robustly, and multiplies most abundantly in that habitat. In the event, too, of a change of climate the species continues to live there longer than elsewhere, and may succeed in clinging to such isolated spots under fundamentally altered climatic conditions long after it has died out from hundreds of other habitats in the neighbourhood. If the species has meanwhile transplanted itself to adjoining territory and established there a fresh area of distribution, the spots where it has managed to survive in the old country appear like lost outposts wrested from the main area of distribution, or like islands lying off the shores of a continent. Such a state of things is by no means uncommon, and we are able to deduce therefrom facts not only concerning the former condition of the vegetable world, but also concerning the climatic conditions which used to prevail and as to the directions in which, in due course, plant-migrations have taken place. We shall have an opportunity to return to these interesting cases in the last chapter of this volume.

It is of great interest to note that the so-called "petites espèces" (see p. 581) of a particular genus often suppress and replace one another in adjacent regions and climatic zones. The first idea which suggests itself to one observing this phenomenon is that the differences of form exhibited by these races in neighbouring districts are the direct result of the diverse conditions of soil and climate under which they exist, and in former times this was the general opinion of botanists. Even at the present day many botanists hold the view that when a plant-species reaches a place where the climatic conditions differ from those of the home it has till then inhabited, it is able to adapt itself to the new environment, that such adaptation takes the form of an alteration of form, that the change is inherited by the plant's offspring, and that in this manner new species arise. But the results of experiments made on purpose to determine this matter do not justify any such opinion. No success has attended efforts to bring back various "petites espèces" to one and the same form by cultivation under precisely similar conditions, nor has any one of those species undergone the anticipated transformation on being transferred to the external environment which was looked upon as the cause of the variation in question. Either the species subjected to the new conditions succumbed thereto and perished without leaving any offspring, or else it underwent such alterations in form as are usually considered to be indicative of varieties merely (see pp. 508–514). These changes were not inherited by the offspring, and no "petite espèce" has ever arisen from a variation caused by properties of soil or climate. Such characteristics as are preserved by heredity, and constitute the essence of a species can therefore only have made their appearance, even in the case of "petites espèces", as a result of crossing. Whenever characteristics produced by a cross were in harmony with the climatic conditions of a district, the survival of the form which possessed those characteristics was assured. Such a form would be able to acquire through its offspring an area of distribution exactly co-extensive with the appropriate conditions of soil and climate. The two old species from which the new one sprang may both remain in the neighbourhood; it is, however, possible for one only of them to survive, and it is also conceivable that both should have died out. We must not forget in dealing with this question that the age of most species is much greater than was formerly considered possible, that in the case of the majority of species repeated displacements of the area of habitation have taken place since the species arose, that in the course of these displacements the species which belong to a single original stock, and are therefore allied in respect of the history of their evolution, have often been separated from one another, and that a proportion of them have perished and vanished altogether from the scene.

So long as two areas of plant-distribution, formed in adjacent zones or regions, do not touch anywhere, intercrossing between the denizens of those areas is very difficult, if not impossible, and even the "petites espèces" persist unchanged under such circumstances, and preserve their specific characteristics in their offspring. But even where the areas of distribution adjoin one another, and the distance between their native species constitutes no hindrance to cross-pollination, it is still possible

for two or more species to remain sharply marked off from one another owing to the fact of their flowering at different seasons. If the flowers of one species are already over when the other begins to bloom, no cross can take place between them under natural conditions. This obstacle to cross-pollination, which has been termed *asyngamy*, is the cause which enables very similar species sometimes to live close together without producing hybrids, and thus prevents the origin of new intermediate forms. For example, when *Aster Amellus* begins to bloom the flowers of the similar plant known as *Aster alpinus* are already over in the same locality, and again, at the season when *Solidago Virgaurea* unfolds its earliest blossoms, the flowers of the allied species *Solidago alpestris*, growing in the same neighbourhood, have already set their fruits. Such asyngamic species, of which mention has already been made on p. 510, are therefore found even in localities where their areas of distribution are contiguous, and even where those areas dovetail into one another, and where the various "petites espèces" grow together and transmit their specific characters unaltered to their descendants.

PLANT COMMUNITIES AND FLORAS.

Wherever the reign of nature is not disturbed by human interference the different plant-species join together in communities[1], each of which has a characteristic form, and constitutes a feature in the landscape of which it is a part. These communities are distributed and grouped together in a great variety of ways, and, like the lines on a man's face, they give a particular impress to the land where they grow. The species of which a community is composed may belong to the most widely different natural groups of plants. The reason for their living together does not lie in their being of common origin, but in the nature of the habitat. They are forced into companionship not by any affinity to one another but by the fact that their vital necessities are the same. It may perhaps be true that amongst the many thousands of plants inhabiting the earth no two are to be found which are completely alike in their requirements in respect of the intensity and duration of solar illumination, the concurrence of a particular duration of daylight with a certain amount of heat, the composition and quantity of the nutrient salts available at the places where the plants live, the amount of moisture in the air and in the ground, or, lastly, the character of the rainfall. This does not, however, exclude the possibility that in particular places similar demands may be met, and that different species with similar needs may flourish undisturbed side by side as men live together in one house or in one town, and, although their customs and their needs may not be exactly the same, yet form a society which is permanent and thrives, and wherein each member feels at home, because it rests upon common usages and is adapted to the local conditions. Nor is it impossible that each one may derive an advantage from the common life,

[1] *Cf.* A. Kerner von Marilaun "Oesterreich-Ungarns Pflanzenwelt", in *Die Oesterreichisch-Ungarische Monarchie in Wort und Bild.* Vol. i. p. 185 (1887).

that the associated individuals may support one another in the conduct of their lives, and that they may even be dependent upon one another.

A knowledge of the communities which exist within the realm of plants is of great importance in many ways. It throws a strong light, not only on the mutual relations of the different species which are associated by common or similar needs, but also on the connection of plant-life with local and climatic conditions and with the nature of the soil. It may fairly be said that in the various zones and regions of our earth no kind of phenomenon so thoroughly gives expression to the climate and the constitution of the soil as the presence of particular plant-communities which prevail, and, accordingly, the determination and description of such communities constitutes an important part of geography. Hitherto, it is true, only a few investigators have paid attention to this subject, and even they have given it but moderate study, the reason being probably that for the determination and description of plant-societies comprehensive data concerning all the species which flourish in the district under investigation are requisite, and the acquisition of such data has been greatly neglected of late years owing to the paramount attractions of other departments of Botany. The small progress of our knowledge in that direction is due also in part to the circumstance that a uniform method of investigating, describing, and classifying plant-communities has not up to the present time been successfully instituted.

The first thing that strikes anyone who takes up this subject is the fact that the different species of plants play very unequal parts in the formation of communities. Certain species predominate in respect of the number of their individuals. They determine the general character of the community, and form the groundwork of the vegetation as a whole, whilst the rest only make their appearance here and there, and look as though they were merely intercalated in the groundwork. It stands to reason that such dominant species, as they are called, belong chiefly to those which by nature grow together in numbers, and that those in particular are the most conspicuous which are aggregated together on a large scale.

Having regard to the dependence of plants upon soil and climate, the nature of which has been fully set forth in the first volume of this work, it might be expected that all plants living under identical conditions would have a common aspect or physiognomy. But this idea is only confirmed in the case of dominant species. The subordinate species may differ from the dominant ones, and also amongst themselves. One of the most usual causes of such differences of form is that the subordinate species of a community pass through the processes of budding, flowering, and fruiting at different seasons relatively, and that one species is adapted to the conditions which prevail in the spring, another to those of summer, and a third to those of autumn. It may also happen that certain reciprocal advantages accrue to neighbouring members of a community from the variety in the forms of their stems, foliage, and flowers. If one species affords at the right moment the shade required by another, or serves as a support for it to climb up, or protects it from high winds, such assistance not only does no harm to the community, but, on the contrary, con-

tributes materially to its preservation; and the same may be said of the cases where a contrast between the colours of the flowers of adjacent species promotes visits from insects, or where any other mutual help is afforded by plants growing side by side in a community. The general aspect of a community is scarcely influenced at all by diversities in the nature of the subordinate species, but depends solely on the dominant species which enter into its composition. These stamp their characteristic aspect upon the entire community, and determine the general impression conveyed to the observer.

This fact is of great moment when we come to the task of identifying, classifying, and naming the various communities formed by plants. Not only must the gregarious dominant species afford the basis of description in the case of each separate community, but their external appearance is the most important means of classifying in groups, according to similarity of aspect, the numerous communities which have been formed in the present period of the earth's history. Observations made under natural conditions, and extending over many years, have led to a division of plant-communities into the following nine groups:—

I. *Forests.*—The dominant species are plants with standard stems (see vol. i. p. 712). In accordance with the common notion of a forest, the stems which constitute its substructure are destitute of branches or leaves up to a certain height. Where this height is not much above that of a man, we speak of a copse; but if the standard stems remain branchless and leafless to a greater height, the assemblage of plants is called a forest proper. We might call these two kinds of forest (for the purposes of this chapter) high forest and low forest, though the terms are not in all ways free from objection; further, the circumstance that high forest has been low forest in the younger stages of its development is an additional reason against their adoption. If the trees of which a wood is composed are so close together that their top leaves and branches are in contact and form a sort of roof, the wood is said to be crowded or dense; whilst, if the trees are so formed and situated relatively to one another as to allow the rays of sunlight to penetrate between them and reach the ground, the wood is said to be thin.

II. *Scrub.*—The dominant species are shrubs, semi-shrubs, and cactiform plants growing in thickets, and never developing standard-stems, but branching from the very base, even when full-grown. The transition is quite gradual from erect scrub, reaching to a height of 2 or 3 metres, to those in which the stems lie upon the ground, and only lift their woody branches a few decimetres above it. It is the nature of shrubs and semi-shrubs to form thickets. Most of the bigger shrubs are impenetrable if not modified by human agency. In special situations, and under certain annually recurring conditions, woody plants of a kind, which usually develop into trees and exhibit standard-stems, may be dwarfed and assume the form of tall shrubs. For example, in the Alps, where trees growing near the boundary-line, beyond which their existence is impossible, are liable to be loaded with heavy masses of snow, and again, in the valleys annually exposed to avalanches, the Beech grows in regular thickets. They are, nevertheless, to be looked upon as forests which have

been dwarfed by peculiar circumstances to the level of low forest. If the uncongenial conditions referred to were to cease, a forest with standard-stems would grow up on the spot.

III. *Plains.*—The dominant plants are perennial and profusely-flowering herbs and undershrubs of gregarious growth. The form, direction of growth, and mode of ramification of the aërial herbaceous stems is always conspicuous, and may even be recognized when the foliage-leaves are of considerable size. Innumerable grades of this form of plant-community exist between Thistles and Umbellifers, reaching a height of 2 metres, which flourish on the Steppes, and the undershrubs scarcely 2 centimetres high, which grow on the débris-slopes in high mountain regions. No sharp line of demarcation can be drawn between them. Nor can any exact distinction be maintained between those Plains in which annuals and biennials and those in which perennial growths predominate. It is, however, possible within certain limits to distinguish between the different types of vegetation under this heading.

IV.—Another type, which may be termed the *frondose* type, has as its dominant plants such as have their stems either entirely subterranean, or else rising but slightly above the ground, whilst from their extremities are developed a crowd of fronds, branch-like leaves, or leaves with large laminæ. The stems are completely hidden by these leafy structures, so that their form and direction and the nature of their ramifications are never clearly visible. This type is conspicuously wanting in flowers. Where flowering-plants also form a constituent part, such plants either have precocious flowers, which have already passed into the fruiting stage by the time the mass of foliage has unfolded, and which subsequently disappear without leaving any trace (e.g. *Saxifraga peltata, Tussilago, Petasites*), or else their flowers are so lost amid the innumerable large foliage-leaves that they do not occasion any material alteration in the general aspect of the plant-community (e.g. *Funkia, Nelumbium*; see fig. 436, p. 775, and most Aroideæ). A special form of this type is exhibited on the surfaces of stagnant or gently flowing water, where discoid foliage-leaves rest upon the water and cover the surface completely. Of it there are several varieties depending on the dimensions of the constituent parts; *cf.*, for instance, Water Lilies and Duckweed.

V. *Ribbon-growths.*—The dominant plants are social hydrophytes with submerged stems and foliage-leaves, or with stem-like or foliaceous thalli. Sometimes forms possessing foliaceous thalli and long, flaccid, ribbon-shaped foliage-leaves predominate, sometimes forms which look like submerged leafy or leafless shrubs, but which differ from real shrubs in that they are herbaceous throughout. A gregarious growth of species with thalli or foliage-leaves which are split up into long narrow segments, or of species whose thalli exhibit a whorled system of ramification may also be present. Ribbon-growths may be separated into various subdivisions, according as one or other of these different sorts of plant predominates.

VI. *Reeds.*—The type is afforded by plants which grow in quantities together and have herbaceous stems of the kind called haulms and scapes. The stems are destitute of foliage-leaves (Horse-tails, Rushes, &c.), or else they bear long, narrow

leaves. Shoots bearing inconspicuous flowers spring up from the species which grow in tussocks, whilst the non-tussock-forming, but more continuously crowded types, develop haulms and scapes bearing an abundance of leaves. The tufted sedges afford an example of the former, and arundinaceous plants of the latter. A reed-like vegetation is developed both on marshy and on dry ground; instances of the latter occur in the Tropics and in Steppe-regions.

VII. *Carpet.*—The typical character is given by low, perennial plants, which form a close mat covering the ground. According as plants with narrow, stiff, grass-like leaves predominate, or such as form a soft, swelling carpet, two types may be distinguished; further, according to the nature of its most important constituents the community may be spoken of as a grass-carpet, herbaceous carpet, moss-carpet, &c. Carpets may grow either on dry or on marshy ground. Sometimes they are restricted to the immediate vicinity of springs or form merely a coating to slabs of rock, but they also spread over wide areas on mountain-slopes and basins. They belong especially to high mountains and to the Arctic regions.

VIII. *Incrustment.*—The dominant species are Thallophytes, which become rigid and brittle when dry or as a consequence of being incrusted with lime. The aggregations of these plants either form solid banks and reefs or else spread in the form of a loose covering over the earth, or they appear as incrustations on rock, earth, or sand. They develop both in the air and under water.

IX. *Felts.*—The dominant species are plants possessing thalli composed of delicate filaments which are more or less entangled together. They may grow in water either in a flocculent form or in coherent felted masses, and they also appear as a thin coating to stones or earth, in which form their characteristic colours render them visible from afar.

The names applied to the above nine classes or types of plant-communities are purposely devoid of reference to the particular alliances, families, or genera concerned in the formation of the communities, because the origin of the latter has nothing to do with the existence of any affinity amongst their constituent plants. Nor has it been possible to take into account the nature of the habitats or the situation of the zones and regions of the earth's surface where the communities grow. This is not the case, however, when we come to name the separate communities which belong to the above classes. For this purpose the use of a name which refers to the habitat, zone, or region where the particular community flourishes, or to the ruling species, genera, or families of which it is composed, is not only inevitable but actually desirable. The most convenient system of nomenclature to adopt here is that which has proved the best in all other descriptive sciences. In accordance therewith each plant-community is designated by two names, one denoting the class to which the community belongs and the other indicating its special characteristics.

In the present state of our knowledge it is impossible to name even approximately the plant-communities which are formed by the aggregation in various ways of some or other of the many thousands of species inhabiting the earth. I

Fig. 481.—Bamboo Forest in Ceylon (from nature by von Königsbrunn).

Fig. 432. — Mangrove Forest in India (from nature by von Ransonnet).

will therefore only make a few observations on the subject, and draw attention to the most striking cases of plant-communities.

The greatest interest naturally attaches to forests which impress the observer by their size, and it is easy to understand why these have always been chosen for the most thorough investigation and description. As regards the species which are either the only constituents of the community, or at any rate its ruling members, we must first distinguish forests of deciduous Conifers and those of evergreen Conifers. A Larch forest (see fig. 354, p. 483) may be taken as an example of the former. Of the evergreen variety there is an extremely large number, owing to the fact that most true Conifers grow in dense forests. A forest of Spruce Firs is represented on p. 415, vol. i., a forest of Silver Firs on p. 717, vol. i., of Scotch Pines on p. 723, vol. ii., and of Arolla Pines on p. 724, vol. ii. Forests composed of Angiosperms are likewise differentiated into deciduous and evergreen. Amongst deciduous forests of this kind the Beech-woods (see p. 761), Birch-woods (see p. 721, vol. i.), and Oak forests (see vol. i. p. 716, fig. 173) of the North Temperate Zone are especially noticeable on account of the characteristic aspect exhibited in each case. Angiospermous evergreen forests manifest their greatest variety in tropical and sub-tropical regions. To the Tropics belong also a number of other special kinds of forest, such as those composed of Euphorbias, Casuarinas, Bamboos (see vol. i. p. 713, fig. 172), of Mangroves (see vol. i. p. 605, fig. 143, and p. 759, fig. 187), and of Palms respectively, whilst many others could be named. Drawings from nature in the Tropics representing Bamboos and Mangroves are also given in figs. 481 and 482.

Scrubs, which are, so to speak, repetitions of woods or forests in little, may be similarly divided into groups. We distinguish between those in which the shrubs and semi-shrubs, which are predominant or in exclusive possession, are leafless and those where the shrubs are provided with foliage. Amongst the social plants of the first group switch-plants and certain cactiform plants hold a prominent place among the other plant types (see vol. i. p. 331, fig. 80). The social plants of the second group are either evergreen or deciduous. The former are furnished with acicular or squamiform leaves which are appressed to the branches (shrubby Conifers and Heaths), or else are clothed with flat, expanded leaves. The case of Alpine Roses (*Rhododendron*) will serve as an example of the second variety. Amongst deciduous shrubs and semi-shrubs which grow sociably and form extensive scrubs we may mention Tamarisks, Spiræas, Roses, Dwarf-Almonds, Dwarf-Birches, Dwarf-Willows, Proteaceæ, Labiatæ, Broom, and Mimosas.

As regards plains we must first distinguish those where the predominating perennial plants have no foliage-leaves, but are furnished instead with green, fusiform shoots and branches of a foliaceous nature (e.g. *Salicornia*). Of leafy plants which occur as predominant members of plains we may mention Umbellifers, Thistles (see vol. i. p. 436, fig. 115), Agaves and Pine-apples (see vol. i. p. 657, fig. 153), and the Asphodel (see fig. 413, p. 729), as the most striking examples. The rest of the social suffrutices may be placed in three groups. The species

belonging to the first group, to which belong in particular many Composites, Caryophyllaceæ, Chenopodiaceæ, Papilionaceæ, and Cruciferæ, are multifariously branched from the very base (e.g. *Artemisia, Gypsophila, Salsola, Melilotus, Crambe*); the species of the second group have upright stems which are unbranched up to the region of the flowers and bear entire leaves (*e.g.* many species of *Verbascum, Epilobium, Œnothera, Euphorbia*), and the species of the third group possess erect stems which have few branches, or none at all, but bear variously lobed and compound leaves (e.g. *Glycyrrhiza, Eupatorium, Tanacetum, Sambucus Ebulus*).

As regards the fourth or frondose type (*cf.* p. 888), we have already indicated certain varieties. In describing the different communities of this kind special emphasis must be laid also on the circumstance of the green laminæ being entire, as in *Petasites, Tussilago, Nelumbium, Asarum, Scolopendrium,* and *Saxifraga peltata,* or divided and incised, as in most Ferns, several Aroids, and a few Hellebores. We must also take into account whether the fronds or foliage-leaves are deciduous or evergreen, as in *Hedera* and *Helleborus niger.*

Ribbon-plants occur in great variety in both flowing and stagnant waters, be they fresh, brackish, or salt. The general aspect of any particular aggregate of these ribbon-like forms varies according to the area and shape of the foliage or thallus of the species concerned, and particularly according to whether the stems or the stem-like parts of the thallus are lax or packed close together so as to form a dense, pulpy matrix. The most conspicuous examples of social species are *Myriophyllum* with pectinate leaves, the Pond-weeds (*Potamogeton*) and Zannichellias with filiform leaves, the Pond-weeds with broad, translucent leaves (see vol. i. p. 551, fig. 136), the Grass-wracks (*Zostera*), *Vallisneria* (see vol. i. p. 667, fig. 155), and *Cymodocea,* also a few of the Mosses (e.g. *Fontinalis*), various species of *Fucus, Laminaria* (see vol. i. p. 588, fig. 139), *Sargassum, Macrocystis,* and *Cystosira* amongst Brown Seaweeds, species of the genera *Ceramium, Callithamnium, Polysiphonia,* and *Lemanea* amongst Florideæ, the species of *Bryopsis* and *Caulerpa* amongst the Siphoneæ, and the several species of *Chara* and *Nitella* amongst Stoneworts.

The points whereon the classification of Reeds is based have been already indicated on p. 888. A number of distinct forms may be distinguished according as particular species of Horse-tail, Sedge, Rush, Restiaceæ, Scirpus, Calamagrostis, &c., prevail. The drawing of a Papyrus-swamp on p. 747 may be taken as typical of this class of vegetation. In the North Temperate Zone, of those which grow on dry ground the most prevalent species are those of the genus *Calamagrostis.* A great many Reeds occur in the Tropics and in the Steppe regions of both the Old and the New World, especially in the pampas, llanos, &c.

The plants which constitute the dominant members of carpet include both Phanerogams and Cryptogams. Of the former the most important are the interweaving and tussock-forming Grasses, Sedges, and Rushes, the interlacing, grass-leaved Caryophyllaceæ (e.g. *Alsine Rosani, Cherleria sedoides, Silene acaulis*), the species of Houseleek (*Sempervivum*) which form rosettes, the Saxifrages of the *Aizoon* group, the loosely-woven delicate Saxifrages which grow near springs,

lastly, Montias. Of the Cryptogams almost all are Mosses, the chief species being the Sphagnums, Polytrichums, the species of *Dicranum* and *Gymnostomum* which grow in dense aggregates, and the Hypnums which cling together in loose mesh-work (e.g. *Hypnum Schreberi*, *Hylocomium splendens*, and *Hylocomium triquetrum*).

Only Lichens, Florideæ, and a few Stoneworts take part in the formation of incrustments. Extreme variety is exhibited by Lichens which combine to form crusts closely appressed to the substratum. The chief dominant plants are various species of *Acarospora*, *Amphiloma*, *Lecanora*, *Lecidella*, *Pertusaria*, and *Verrucaria*. The best-known and most widely-distributed incrustment is that which is formed by *Lecidea geographica* or *Rhizocarpon geographicum*, and imparts a characteristic colour to the blocks of stone on slaty mountains. A looser type of incrustment is composed of various fruticose Lichens, principally of Cladonias and Cetrarias, and are most striking in high mountains and in the Arctic tundra. A less important form is one composed of submerged Characeæ and Florideæ incrusted with lime, *e.g.* by species of *Corallina*. The lime-incrusted species of *Lithothamnium* and *Lithophyllum* which combine to form solid bank-like incrustations known as nullipore-banks only occur in the sea.

Felts are formed by filamentous Algæ. The dominant plants are Scytonemaceæ, Conjugatæ, Ulotrichaceæ, Œdogoniaceæ, Vaucheriaceæ, and a few others. The Conjugatæ, such as the various species of the genus *Spirogyra*, fill stagnant ponds with their green filaments; several of the Vaucheriaceæ grow in closely felted masses in water-courses or on damp earth, and several Scytonemaceæ and Confervoideæ weave themselves into thin mantles over stones. Felts are but seldom of very conspicuous appearance. The best known is the thin felt formed by *Trentepohlia Iolithus*, to which is due the red coloration of blocks of stone ("Violet-stone") seen in mountain regions.

It is only in rare cases that a plant-community is composed of a single species alone. For the most part two, three, or even more species of similar aspect are jointly predominant. At the same time it may happen that at one spot one species, at another spot another species is kept in check without any material alteration being thereby incurred in the general appearance of the particular community. Thus, for instance, the slopes of the schistose mountains of the Central Alps are clothed with carpets in which *Carex curvula*, *Juncus trifidus*, and *Oreochloa disticha* are dominant species. Here and there these three species share equally in the composition of the carpet, but in many places one is paramount, whilst the others sink into the background, so as to be scarcely noticeable at first sight. No further explanation is requisite to show that in such cases the community must not be named after one only of the dominant species.

As regards the subordinate species of a community it would be a great mistake to suppose that their occurrence is subject to no sort of rule. Though they seldom have any striking influence on the *tout ensemble* of the community their importance in it must not be under-estimated. Many of them are so constantly associated with

certain gregarious species that, where a plant of the one kind occurs, the presence of its companion species of the other kind may be inferred with certainty, and obviously due regard must be paid to such constant companions in any description of particular communities. A further circumstance which must not be overlooked is that up to a certain point the subordinate species may replace one another. Thus, for instance, that variety of carpet in which the Mat-grass (*Nardus stricta*) forms the dominant species, includes as subordinate species both in the Alps and the Carpathians *Homogyne alpina*, *Hieracium alpinum*, *Campanula Scheuchzeri*, &c. Certain other subordinate species, e.g. *Potentilla aurea*, *Hypochœris Helvetica* and *Campanula barbata*, which are almost invariably present in the community in question when it grows in the Alps, are, however, replaced in the Eastern Carpathians by *Potentilla chrysocraspeda*, *Scorzonera rosea*, and *Campanula abietina*.

Special attention must be drawn to the fact that species which are gregarious in one plant-community occur as a mere sprinkling in another. When this observation is first made in Nature it is apt to lead one to suppose that it is a vain task to attempt to arrange the different communities in groups, and to define and describe each separate kind. But more careful study soon convinces one that the phenomenon in question, far from interfering with the scientific treatment of the subject, actually assists it, and that the history of plant-communities is elucidated thereby. It has been repeatedly remarked that mud newly deposited by water, exposed soil, and naked rock do not forthwith deck themselves in their permanent mantle of vegetation, but that first of all small Algæ, Lichens, Mosses, and various annual Phanerogams establish themselves and prepare the way in the course of time for other plants. This preparation, which was described in vol. i. pp. 257–268, consists not only in mechanical changes in the ground, but also in the admixture of humus derived from the parts of the first settlers which die off. The only species which take possession of ground so modified are such as differ entirely from the first colonists, and, curious to relate, the latter are gradually ousted by the new arrivals and driven from the field. But the second settlement has no permanence either. The quantity of humus arising from the death of plants increases from year to year, the soil becomes too rich for the plants in possession, and the process of eviction is now undergone by them at the hands of fresh species, which thrive on the rich soil, and gradually possess themselves of it. At least three successive series of settlers may thus be traced on every spot, and not infrequently the number is four or five. Now, if each of these groups corresponds to a particular community, which is as a matter of fact the case, the phenomenon described must produce the same impression as though the communities became transformed into one another in course of time. It is therefore necessary to recognize the existence of the incipient and decadent stages as well as that of predominance. In the incipient stage relics of the community which previously occupied the same spot are still to be found, and in the stage of decadence the first pioneers of the community that is to succeed make their appearance. When, for example, a carpet is invaded here and there by individual plants belonging to species indicative of communities which pertain to some other type,

such as scrub or plain, the occurrence does not in the least confuse the definition and description of the carpet. It only shows that for purposes of determination and description, whilst attending primarily to the stage of the community when development has reached its zenith, we must also take into account in each case the stages of incipience and decadence, and the relations to other communities.

Wherever the configuration and composition of the ground favour the formation of various kinds of habitat within narrow limits of space, there the particular plant-communities which correspond to those habitats develop in great variety close together. The boundary-lines of adjacent communities are disposed in a multitude of different ways in such cases. In lowlands where gentle hills alternate with shallow depressions, and where from sand one passes to clay, and thence, perhaps, to ground covered with saline efflorescence, the communities are not infrequently pieced together like the components of a mosaic. In other places those which cover a small area are interspersed like islands in the midst of the more extensive communities; and, again, in other cases the different areas are in the form of contiguous strips and zones. The last mode of distribution occurs chiefly along the margins of still or running water, and is explained by the uniform diminution of moisture in the ground as the distance from the water's edge increases, and in the case of still water also by the tendency of plants to advance from the margins towards the middle of the expanse of water where they grow, or, in other words, from the continuous transformation of the ribbon types which flourish in water into reeds, of reeds into plains, and of plains into carpets or into forests.

It very often happens that two or more plant-communities are intermingled, and that the whole exhibits a kind of stratification. A pine forest may exist by itself, that is to say, it may include nothing but dominant pines with, perhaps, a sprinkling of a few other kinds of tree, and the ground may be bare except for a bed of dry fallen needles. On the other hand, a carpet may have developed on the forest floor, whilst, in addition, a Bilberry scrub, a low scrub of *Calluna vulgaris* or *Erica carnea*, and a high scrub of Juniper may have obtained a footing, all of which communities are capable of existing independently without the shelter of the pines, and are often met with thus alone. But although the presence of the one community is not indispensable to the existence of the other, the fact of their occurring together shows that no injury is suffered on either side in consequence of the companionship, and it is much more likely that communities growing on the same ground are mutually helpful and protective. In many cases there is no doubt of this, as, for example, when a community of tall plants develops on soil previously prepared by a community of low plants without completely ousting them. We gather, then, that the conjunction of several communities is by no means fortuitous, that the association is always between certain particular communities, and that even here we find strict orderliness and subjection to definite laws.

Unions of communities formed in the manner above described have been termed *plant-formations*, probably from analogy with the combinations of strata of earth and stone which geologists call formations. The selection of this name is not quite

fortunate, but having been once introduced into the science, it must remain, and it is only necessary to point out that the communities united in a formation do not always exhibit any obvious stratification. Thus, for instance, in many tropical forests (see fig. 420, p. 741) communities are interpolated which belong to the most widely different types, and exhibit all possible grades in respect of the height to which their component plants grow. These communities occupy sometimes only a restricted area, sometimes a considerable expanse either down on the ground or midway between the ground and the tops of the trees; and, moreover, in all such formations there is always a sprinkling of climbing-plants and epiphytes, which make it quite impossible to discover distinct strata. In many other cases, it is true, the communities constituting a formation are in obvious strata. If we may compare the plant-formation to a building, the communities may be said to form the stories rising one above the other. Sometimes only two communities are superimposed on one another, sometimes it is possible to distinguish three or more strata or stories. There are formations in which each story belongs to a different class of community, but others exist also where two or three of the stories are of the same class, as, for instance, where several scrubs rise one above another, or where two forests are united, so that the crown of one species of tree forms an upper tier, and that of another species a lower tier.

The names of the different plant-formations should be chosen with regard to the community which forms the roof of the entire edifice of plants in each case, and which, therefore, projects above, and, in a sense, prevails over all the other communities.

At the beginning of this chapter stress was laid on the fact that every region receives a characteristic impress from the nature of the plant-communities inhabiting it, and that a knowledge of the latter is consequently of great importance in descriptive geography. The remark has also been made more than once that the particular conditions of soil and climate in a locality find expression in plant-communities, as it must be presumed that the species characteristic of each community can only grow in masses at places where the composition of the soil and the conditions of illumination, temperature, and humidity are in harmony with the specific organization as a whole. But if the local conditions of the ground and climate are reflected in the plant-communities, it is equally the case that the distribution of the plant-communities and formations constitutes an important and perhaps the only available basis for a division of the earth into natural floral areas. We proceed on the principle that every district possessing a series of plant-communities which are peculiar to itself is to be treated as a floral area, and that a limit to such area occurs at every place where the characteristic communities of a particular floral area are threatened with destruction, and, therefore, encounter the natural boundary of their range, where other communities better adapted to the altered external conditions make their appearance, and where there is consequently a change in the aspect of the whole landscape. This also supplies the scheme for a scientific geography of plants. Unfortunately we are still far from possessing any such science. We have only a

scanty knowledge of the plant-communities of Central and Northern Europe, and in many extensive tracts as good as nothing is known concerning the most important of all the data required for a demarcation of floral areas. There is nothing for it, therefore, for the present but to grope along with the help of the little that has been ascertained, and in the case of many districts to retain the demarcations laid down by earlier investigators, notwithstanding the fact that they are based upon altogether different foundations.

According to this system, the various Floras may be roughly distinguished as follows:—

1. **Arctic Flora.** The northern parts of Europe, Asia, and North America, extending southwards about as far as to the Arctic Circle.
2. **Baltic Flora.** Scandinavia, Great Britain, North-German Lowlands, Western Russia encroaching to the south on the Floras of the Mediterranean and Black Sea.
3. **Flora of the Black Sea.** South-eastern Europe, Asia Minor with the exception of its southern and western shores, the Caucasus, Kurdestan, Persia: environs of the Caspian Sea.
4. **Mediterranean Flora.** Shores of the Mediterranean: Southern Europe, the western and southern shores of Asia Minor. Coasts of Syria, Egypt, Tunis, and Algiers.
5. **Atlantic Flora.** Azores, Canary Islands, western shores of the Spanish Peninsula, Morocco.
6. **Siberian Flora.** The plain extending from the river Obi and its sources to the Stanovi Mountains.
7. **Kamschatkan Flora.** North-east Asia as far south as the region of the Amur River.
8. **Amur Flora.** Amur district, Manchuria.
9. **Chinese Flora.** China, Japan, extending nearly as far south as the Tropic of Cancer.
10. **Flora of Central Asia.** Mongolia, Thibet, bounded to the west by the Steppe-region of the Sea of Aral, and to the south by the Hindu Kush and the Himalaya.
11. **Flora of South Arabia and Mesopotamia.** Northern shores of Somali, South Arabia, Mesopotamia; shores of the Persian Gulf.
12. **Sahara Flora.** The Sahara to about 15° N. Lat., Northern Arabia.
13. **Soudanese Flora.** Bounded on the north by the Sahara, on the south by 10° N. Lat., to the east by the mountainous region of Abyssinia.
14. **Flora of Guinea.** From 10° N. Lat. to 10° S. Lat., eastwards to 35° E. Long.
15. **Zambesi Flora.** From 10° S. Lat. to the Orange River on the south, and bounded to the east by the Drakenberg Mountains and Lake Nyassa.
16. **Abyssinian Flora.** Abyssinia and the mountains adjoining it on the south.
17. **East African Flora.** From the shores of the Indian Ocean to the East African Mountains, northwards as far as 8° N. Lat.
18. **The Cape Flora.** The south-western part of the Cape, bounded to the north by the Great Karroo Desert.
19. **Madagascan Flora.** Madagascar.
20. **Indian Flora.** Bounded to the west by the Indus, to the north by the Himalaya and the Yunnan mountains, and extending eastward as far as the Straits of Lomboc and Macassar.
21. **Pacific Flora.** Pacific Islands from the Moluccas to the Marquesas Islands on the one hand, and from the Sandwich Islands to New Zealand on the other.
22. **Tasmanian Flora.** Victoria, Tasmania, New South Wales, and adjoining regions.
23. **Australian Flora.** Interior and Western Australia.
24. **Canadian Flora.** Bounded to the north by the Arctic Flora, and reaching westward as far as the Rocky Mountains, and southward as far as the North American Lakes.
25. **Columbian Flora.** Bounded on the north by the Arctic Flora, on the east by the Rocky Mountains, on the south by 50° N. Lat.
26. **Mississippi Flora.** Extending northward to the Lake region, southward to Florida, exclusive of the southern third of that Peninsula, and bounded to the west by 95° W. Long.

27. **Missouri Flora.** Region of the Missouri River and of the high land between the Rocky Mountains and the Cascade Mountains.
28. **Flora of the Pacific Slope.** Coast region west of the Cascade Mountains, California.
29. **Texas Flora.** Arizona, Texas, North Mexico.
30. **Mexican Flora.** Mexico as far as Nicaragua.
31. **Antilles Flora.** The Antilles and the Bahamas, southern extremity of Florida.
32. **Brazilian Flora.** Bounded to the west by the Andes from the Gulf of Guayaquil to Tucuman, extending southward to 30° S. Lat.
33. **South American Flora.** Coast land west of the Andes and the part of South America between 30° and 50° S. Lat.
34. **Magellan Flora.** The extremity of S. America from 50° S. Lat., excluding the high mountains.
35. **Antarctic Flora.** Antarctic Islands, high mountains of the southern extremity of South America.

In this outline only a passing reference has been made to the Floras which at present occupy the higher regions of mountain chains, and which are restricted to comparatively small areas. Yet there is often far more difference between these and the Floras of the lower parts of the mountains and of the adjacent plains than there is between Floras which exist side by side in the lowlands, and are usually scattered over wide areas. Thus, for example, the Flora of the high mountains of Central Europe, commonly known as the Alpine Flora, differs so utterly from the Baltic Flora developed to the north of the Alps, and from the Mediterranean Flora flourishing to the south on the shores of the Mediterranean Sea, that it could not be classed either with the one or with the other. The same phenomenon is observed in other regions where lofty mountains occur, and, probably in addition to the thirty-five Floras above mentioned, as many more high-mountain Floras might be distinguished. The importance of these mountain Floras in relation to the formation of the Floras of the plains and to the general history of the plant-world will be set forth in the next section.

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5 THE EXTINCTION OF SPECIES.

In the portion of this work which dealt with the origin of species, the view was taken that the new species which make their appearance in the course of ages are the products of cross-breeding between previously existent species. Valuable support is given to this opinion by facts relating to such genera as are represented in one district by a large number of species, and in another by a single species only. In many cases the wealth of forms comprised by a genus is prodigious. It is no easy matter to bring the numerous species of such a genus under review in a single series, because they are connected not only lineally, but also collaterally amongst themselves in all sorts of ways by intermediate forms. Within these generic spheres new forms continue to spring up in our time, and these are proved to be the results of crossings. For example, the multiplicity of forms included in the Bramble-genus (*Rubus*) is extremely great in Central Europe.

Botanists of the old school supposed the reason of this to be that the species of *Rubus* vary from some unknown cause—presumably from an intrinsic tendency in themselves. At the present day no intelligent observer doubts that many of the plants thus set down as the results of mere spontaneous variation are species which arose by inter-crossing in comparatively early times. Such inter-crossing was rendered possible by the fact that in the course of those displacements and alterations affecting floras, to which the present distribution of plants must be attributed, several species of *Rubus*, which had survived from previous periods, met and settled down together in Central Europe. On the coasts of Dalmatia and Greece, where only a single species, viz., *Rubus ulmifolius*, Schott (= *R. amœnus*, Portenschlag), established itself when the changes in question took place, there was no possibility of any multiplication of forms. From that solitary species sprang descendants which never changed; in other words, the specific marks of *Rubus ulmifolius* remained permanent in the above-mentioned parts of the Mediterranean floral area. The idea of the old school of Botanists was that this particular species of *Rubus* had no inclination to evolve new species; or, to use the more erudite but still less intelligible mode of expression, it was destitute of any tendency towards differentiation. The proper explanation of the fact is, however, much simpler and more natural. In the region where this particular species of *Rubus* is settled, there is no possibility of new species of that genus arising by means of inter-crossing. Perhaps some future displacements of floras will bring *Rubus ulmifolius* into proximity with other species of Bramble, and in that case it is sure to take part once more in the generation of new species. If, on the other hand, some event should cause the extermination of the entire Bramble-flora in the adjacent districts, and *Rubus ulmifolius* should remain isolated, no new species will spring from it any more than hitherto. A completely isolated species may continue to reproduce and multiply sexually and asexually for centuries without exhibiting any alteration, provided that the conditions of climate and soil are congenial to it, but it cannot take any part in the production of new species. If at length destruction befall such a species—a by no means impossible contingency, as one change of climate succeeds another, and causes fresh displacements of the limits of plant distribution—the event would connote the extinction of the whole genus of which this species was the sole surviving representative.

The result of comparative researches has been to show that the extinction of single species frequently occurs, whereas such groups of species as Botanists designate by the name of genera rarely die out. By far the greater proportion of the plants whose remains have been preserved from former periods in a fossil condition belong to genera which are represented by plants still living at the present day; only many of the extant representatives differ specifically from those which existed long ago. We conclude that the living types replace extinct ones and have entered upon their parts in life. It is also worthy of note that the fossil remains are often found at entirely different places from those inhabited by their nearest relatives in modern times.

The most striking examples of genera that have become extinct are afforded by the alliances to which the Club-moss and the Horse-tail respectively belong (see pp. 713 and 716). Those genera most exposed to the danger of extinction are such as are only represented by a single species (termed *monotypic* genera). This risk is intensified if the species in question only occurs in one district, as is the case, for instance, with *Welwitschia*. The genus *Rhodothamnus* of which only one species, *R. Chamæcistus*, lives at the present day, and the genus *Azalea* which is, so far as we know, represented by the species *A. procumbens* (*Loiseleuria procumbens*) alone should, on the other hand, have a better chance of escaping extinction. For the area of distribution of the former is broken into two sub-areas by the broad stretch of land reaching from the Eastern Alps to the Altai Mountains, whilst the *Azalea* grows not only on the high mountains of Central and Southern Europe but also in the Arctic regions, leaving a great space between the two areas uninhabited by its kind. Thus, presumably, even if such a species were to vanish entirely from one of its sub-areas of distribution in consequence of changes in climatic conditions it would still be represented by individuals growing at some spot which, being remote from that sub-area, would in all probability not have been affected by the alterations in question.

The number of species that have died out is extremely large. Every group of species which comprises both living and fossil members affords instructive examples in this connection. It is assumed that of species now living the endemic kinds have their existence most seriously menaced, or, in other words, are exposed to the most speedy extinction. If the restricted areas of the South-eastern Alps, where *Wulfenia Carinthiaca*, the most famous of the endemic species, is native, were to undergo a change of climate which no longer permitted the propagation of that species either by sexual or asexual methods, and at the same time rendered its migration impossible, it would be only a matter of time before *Wulfenia Carinthiaca* disappeared completely from the face of the earth. The genus *Wulfenia* would not, it is true, thereby become extinct, for a second species named *Wulfenia Amherstia* occurs in the Himalaya. But as this species, too, is endemic it might easily be overtaken by the same fate, and then the entire genus would have died out. It is, however, conceivable that the change of climate supposed to affect the South-eastern Alps, instead of causing the extinction of *Wulfenia Carinthiaca*, might result in the expansion of its area of distribution, and that no such hindrances to its migration as at present prevail should exist. The two species now inhabiting such widely remote districts might then conceivably come together and cross with one another, with the result that new species would be produced in the genus *Wulfenia*. It will be seen from these examples that one cannot be too cautious in dealing with assumptions concerning the future destinies of species. Many endemic species are probably doomed to extinction in the near future; but it is also not impossible that they may instead be called upon to play an important part in days to come.

An account has already been given (pp. 590, 592) of the manner in which nature affords compensation for the extinction of species, and how new species, the

products of crossing, take the place of the parent-stocks, so that the only remark that need be added here is that when such substitution is observed in the case of plants belonging to successive geological periods, it seemed as though a gradual re-casting or moulding of the species had taken place, and was regarded as a phenomenon determined by the direct effects of variations of climate until the time when the great importance of crossing in relation to the genesis of new species began to be recognized.

The partial extinction of a species, *i.e.* its disappearance from particular parts of its area of distribution, must be distinguished from complete extinction. Of the numerous instances of partial extinction within our knowledge some have been due to intentional or unintentional extermination by mankind, but the majority are cases where purely local extinction has resulted from natural causes independently of human influence. Reference has repeatedly been made in these pages to cases of plants which grow in the midst of now reigning floras and yet do not belong to them, and they have been likened to outposts left behind by former occupants of the soil, being apparently the remains of floras which formerly flourished on the areas in question, but which have been turned out and forced to take refuge in neighbouring regions. If their displacement were due to climatic vicissitudes it is conceivable that separate species or even entire communities may have been left behind here and there in especially favourable, though possibly very restricted habitats, and such isolated spots then seem as though they had been wrested from the main area of distribution which stretches over a wide expanse of country in the vicinity. Interesting examples of this are afforded by several species which are confined to isolated habitats in Carniola, of which the "Königsblume" (*Daphne Blagayana*) may be selected as a type. This plant grows on the slopes of some mountains in the neighbourhood of Laibach. Before the flora of the Balkan Peninsula had been accurately explored it was believed that this species of *Daphne* had no other habitat than that on the mountains above mentioned. More recent botanical researches have, however, revealed the fact that the main area of distribution of *Daphne Blagayana* is really in the Balkan Peninsula, in Bosnia and Servia, and that the habitat in Carniola is to that area as an island to the mainland. When one sees by what a small number of individuals, amounting to some thousands only, this curious plant is represented in Carniola, and how rare it is for even these to bring fruits to maturity owing to the fact that autogamy is impeded and that the supply of insect-visitors is insufficient, there is no escape from the conviction that a series of very severe winters would be enough to cause its complete extermination in this district. Under such circumstances its existence in the main area of distribution in the Balkan Peninsula might not be in any way imperilled, for it is not likely that the particular causes to which the extinction of the species in the small area in Carniola would be due would operate in all the habitats in the larger area, which is hundreds of kilometres away.

That such phenomena as have here been suggested as possible and even probable in the case of *Daphne Blagayana* do actually happen is evidenced by the plant-

species which in one district form a considerable part of the flora in possession at the present day, whilst in another floral area they are only found in the fossil state and under conditions which leave no doubt that they formerly lived there, but have long died out. *Rhododendron Ponticum*, for example, is an important constituent of the flora which now flourishes in the neighbourhood of the Black Sea, and is also found far to the west in an unrestricted area in the South of Spain at a great distance from the main area of distribution. It is encountered in the fossil state on the southern slopes of the Solstein chain in Tyrol in the upper strata of the so-called Höttinger Breccia. Thus this plant must have ranged formerly through Southern and Central Europe to 47° N. Lat. In the South of Spain it has survived on an isolated spot, whilst in the Northern Dolomites it has died out. A similar instance is offered by the case of several Juglandaceæ which form part of the woods of North America at the present day, and are only found as fossils in Europe.

The results of researches into the history of the separate species constitute the foundation for a history of the entire plant-world. Formerly the discovery of fossil-remains was looked upon as the most important means of eliciting that history, but now the distribution of living plants is taken into account, and the significance of such circumstances as the presence of endemic species and of species isolated in the midst of a foreign flora is fully recognized. A study of endemic species and of outlying sub-areas of distribution yields in particular most valuable information concerning the conditions which prevailed in the earliest periods of the earth's history. The most noteworthy inference made in this connection is that over a great part of central Europe since the last ice-age a flora was evolved which was only capable of existing under the influence of a continental climate of far greater warmth than now prevails. For instance, plants whose main areas of distribution at the present day are in the steppes of Southern Russia, in the Crimea, and in the valleys of the Caucasus are found growing, sometimes alone sometimes in communities, in Central Europe, in the region of the Baltic Flora, on warm, sunny mountain-slopes, and in sequestered glens far from the modern lines of traffic, and under circumstances which exclude all possibility of an immigration having taken place in recent times. Such exceptional habitats of the plants in question occur on hot, sombre rocks of serpentine in Lower Austria, on terraces of loess and mountains of schist, situated on the eastern border of the Böhmer Wald and the Mährische Gebirge, in the interior of Bohemia and westwards on scattered spots as far as the Harz Mountains, and, again, in the region of the Northern and Central Alps, from the Wiener Becken to the Lake of Constance, as, for example, far away in the highest parts of the valleys of the Adige and the Inn. These plants may be for the most part described as Steppe-plants, and if, as can no longer be doubted, they are the remains of a flora which once ranged in Central Europe as far as the Harz Mountains, we may conclude that just before the establishment of the present climatic conditions which suit the Baltic Flora, a Steppe-climate prevailed over the area referred to, and the summer was hot and dry. There is good ground for supposing that the various animals belonging to the Steppe-fauna (Steppe-antelope, Steppe-marmot,

&c., *cf.* p. 462) which have been discovered in Central Germany are relics of this period, that they lived with the Steppe-plants and withdrew eastward at the same time in consequence of the change of climate. It is difficult to say when these changes took place in Central Europe, but this much is certain, that the Steppe-climate prevailed for an exceedingly long time, that the alteration of that climate into the kind which now prevails took place quite gradually, and that accordingly the migration of the Steppe-flora and fauna into the region now occupied by them was performed very slowly.

As the very thing which is injurious to the members of one flora is usually beneficial to those of a neighbouring flora the migrations of plants really take the form of displacements of the boundaries of distribution. No sooner do the species of one flora withdraw to escape a climate that has become unsuitable to them than their place is taken by those members of the neighbouring flora which are adapted to the new climate. In the case above referred to, an immigration of such members of the Baltic flora as prefer a comparatively cool, moist summer would inevitably take place synchronously with the retreat of the Steppe-plants. As regards the situation of the previous home of these Baltic plants there can be no doubt. They came from adjacent regions where the climatic conditions congenial to them already existed, that is to say, from parts then forming the coast and from those mountains which had not been ascended by the Steppe-flora. In advancing inland from the coast and descending from the mountains these plants were only in a measure retracing their steps to places where they formerly occupied the ground, and from which they had been ousted by the Steppe-plants. In other words, before the reign of the Steppe-flora of the Black Sea was established in the valleys and lowlands of Central Europe another flora lived there which closely resembled that which we now call the Baltic flora. No approximate estimate can be given of the length of time, previous to the immigration of Steppe-plants, during which the Baltic flora was in possession of the tract of country thus destined to fall a second time under its dominion; but it has been established beyond question that it was not as yet upon the scene at the period of the greatest prevalence of glaciers in Central Europe, and that its first immigration cannot have taken place until after the retreat of the large glaciers.

At the epoch when glaciers attained their maximum dimensions the places now covered by the forests of Pines and Firs, which are so characteristic of the Baltic flora, and by vast scrubs of heaths and broom, were occupied by low Alpine plants which may for the sake of brevity be spoken of collectively as an Alpine Flora. Formerly botanists were of opinion that this wonderful flora spread southwards like a flowing stream from the Arctic Regions at the epoch in question. This view is not, however, in harmony with more recent discoveries. It was based on the erroneous assumption that the flora of the Arctic Regions was the same as that of the alpine regions of Central and Southern Europe. When we compare the Arctic and the Alpine floras merely by means of their records in books and herbaria, it does indeed look as if the closest relationship existed between the two: for a not inconsiderable

number of species belong to both floras, and are only lacking at the present day in the broad tract interposed between the Alps and the Arctic Regions. But of these species common to both floras the majority are distinguished in the Alps by their rarity, and only grow on particular spots here and there on black earth or peat, or close to cold springs. Many must be the botanists who have rambled year after year over the Alps collecting flowers without ever coming across such species as *Saxifraga cernua, Betula nana, Juncus arcticus*, and *Juncus castaneus*, which are common in arctic areas of vegetation but very rare in the Alps, though they may have climbed all the summits high and low, and searched the most sequestered valleys, and, moreover, may possess a thorough knowledge of Alpine vegetation. Similarly, when a Botanist, who has acquired on the spot an accurate knowledge of the Arctic Flora, pays his first visit to the Alps an entirely new world meets his gaze. Not only is the number of species indigenous to alpine regions much larger than that found in the extreme north, but the two floras differ widely in their composition. The very species which are of most common occurrence in the Alps, and which constitute the ground-work of the communities characteristic of that region, are alien to the Arctic Flora. Such are the extensive meadows of Grasses and Sedges, the low-growing forests of Mountain Pines, Alders, and Dwarf Medlars, the scrub of Alpine Roses (Rhododendrons), and the carpet of prostrate woody plants (*Rhamnus pumila, Daphne striata, Salix retusa, S. Jacquiniana*), besides many other species which are peculiarly adapted to a substratum of rock or débris, and constitute one of the chief glories of the Alps. To this category we must also add the particular plants which, next to the Alpine Roses, are the most commonly recognized representatives of the Alpine flora, viz. *Valeriana celtica, Meum Mutellina, Primula Auricula, Artemisia Mutellina, Gnaphalium Leontopodium* (the Edelweiss). The alpine species of more than 50 genera do not grow at all in the arctic regions, and in the case of many other genera, though both districts possess a few of the species in common, it is just those which are peculiarly characteristic of the Alpine Flora that one seeks for in vain in the extreme north. It would thus be absurd to suppose that such a flora has migrated from the arctic regions to the Alps, and there is much more reason for concluding that the scanty flora of the arctic region was in part derived from the high mountain areas of more southern latitudes.

Researches into the subject of the distribution of Alpine species and of the genera to which they belong have revealed the fact that some alpine plants occur also in the higher parts of the Carpathians, in the Caucasus, in the Altai Mountains, and even in the Himalayas, whilst others are found in the Abruzzi and the Balkans, and upon these data might be based the hypothesis that the alpine flora was derived from the east and south, and migrated in the Diluvial Period from the Himalayas, the Caucasus or the Abruzzi to the Eastern Alps. But the same facts might equally well lead any one who made a similar investigation of the Alpine flora of the Caucasus or the Himalayas to infer that the plants in question had travelled thither from the Alps. I believe that all such hypotheses involve one in a circle, and bring one no nearer to the goal. If we wish to solve the question as to what was the place of origin of

the plants which took possession of the ground whence glaciers and snow-fields retreated after the great diluvial ice-age, it is not necessary to look so far afield. We need only bear in mind that in the period preceding that in which the glaciers attained their maximum size in the higher mountains of the Alps, a flora must have existed there, and that this flora would have been forced down from the higher to the lower parts of the mountains and into the sub-alpine regions by the climatic vicissitudes which occasioned the glacial condition. In the Tertiary Period the diminution of temperature accompanying an increase of elevation was doubtless not materially different from what it is at the present day. The general relief of the Alps was the same in the Miocene period as it is now; also in the Eocene period, and even in the more recent portions of the Cretaceous period the Alps were already a considerable mountain region including probably some high peaks. The Limestone Alps had their fjords, and the Central Alps were deeply cut into by cross valleys. The vegetation clothing the lower slopes could not be the same as that of the higher regions, but, as at the present day, there must have been several floras situated one above the other. Glaciers must have existed in a latitude of from 46° to 48° at an elevation of 3000 metres in the highest depressions in the mountains, and that at so small a distance as 50 kilometres from the sea-coast, and subject to a yearly variation in temperature of 8°–10° Centigrade; and even though woods of Laurels and Myrtles flourished in the latter part of the Miocene period of South-eastern Europe on the spurs of the Alps on the margin of the Wiener Becken, that does not exclude the possibility of an Alpine flora having developed simultaneously on the snow mountains of that neighbourhood, and on the Rax-alp and the Hochschwab (in the mountains of Northern Styria). The Carniola Schneeberg to the north of the Gulf of Fiume affords quite sufficient proof that even a mountain of only 1800 metres may harbour Laurels and Evergreen Oaks at its feet, whilst alpine vegetation flourishes on its summits.

The fossil remains of the Miocene flora that are known to us were all discovered in lowland places, and they therefore only represent the plants belonging to gently undulating ground or growing on quite low mountains, and no inferences can be drawn from them as to the nature of the vegetation of the higher regions. I think that we may fairly deduce the conclusion that the majority of the alpine species lived on the heights of the Alps as long ago as in the Miocene period, and that the Alpine Flora though repeatedly forced down to lower levels, always returned again. As a matter of course the composition of the Alpine Flora underwent many changes in the process. The partial intermixture of species belonging to adjacent floras with the alpine species, which must inevitably have taken place in the course of these displacements, led to inter-crossing and consequently to the production of new species, whereof a proportion were no doubt adapted to the altered climatic conditions and capable of preserving their existence. On the other hand, many of the species which already inhabited the Alps in the Miocene Period have died out there or have only survived at isolated spots of limited area, as, for instance, *Wulfenia Carinthiaca* (see p. 882) in Carinthia, and *Rhizobotrya alpina* on the

Fassa Alps in Tyrol. This holds especially in the case of the majority of those species which belong both to the present Arctic Flora and to the present Alpine Flora. Let us suppose the Alpine Flora driven as far as the North of Germany at the time of the greatest distribution of the diluvial glaciers. Extensive glaciers had also advanced far to the south from the north, and had caused a displacement of the flora indigenous to the Scandinavian Mountains in the Tertiary period as far to the south as Northern Germany. Thus the floras of the north and of the Alps must have met there, and when later the climate again became milder a retreat of the immigrants took place on the one side towards the north, on the other side towards the Alps. On this occasion some species which previously did not occur in the Scandinavian Mountains travelled northward, and some hitherto unknown in the Alps travelled into the Alps. To that epoch must be ascribed the introduction into Germany of several Arctic species, e.g. *Alsine stricta, Saxifraga Hirculus, Pedicularis Sceptrum, Statice purpurea, Salix depressa, Betula humilis,* and *Juncus stygius*—which then became dispersed over the low lands lying at the foot of the Alps in Salzburg and Bavaria, though they did not reach the Alpine region, but remained behind on the northern border of the mountain area.

The remarkable relations above referred to as existing between the Alpine flora of the Alps and those of the Carpathians, the Caucasus, the Altai, and the Himalayas, and also those of the Pyrenees, the Abruzzi, the Dinaric Mountains, and the Balkans cannot be explained by what took place in the Diluvial period. It has been ascertained by geologists that the first glaciation of the Alps was not more recent than, but was possibly even prior to, the third stage of the Miocene Period in the south-east of Europe, and that during that epoch there could have been no connection between the high mountain flora of the Alps proper and those of the Carpathians and the Balkans, not to speak of the mountains lying further to the east or south, even though the Alpine flora may have descended to a much lower level on the eastern side. The high mountain floras have hardly met one another either in the direction of east and west, or in that of north and south. If, therefore, in the Alps, after the retreat of the glaciers, other species joined forces with those belonging to the Alpine flora which returned once more to higher regions, these were species belonging rather to hilly lowlands. Many such species are able to endure the alpine climate without being injured, and they are represented even at the present day by large numbers of individual plants both in the lowest parts of the valleys and on the heights of the Alps. Thus *Erica carnea, Globularia cordifolia,* and *Biscutella lævigata* may be traced from the shores of the Adriatic and the banks of Lake Garda, and from the less lofty heights on the border of the Wiener Becken up into the alpine region, and may be looked upon as representatives of the plants which naturalized themselves in that region after the last diluvial ice-age.

If the kinship of the floras growing on the crests and shoulders of the high mountain chains which succeed one another from west to east and from north to south is not explicable from what took place in the Diluvial period, we must go back to an earlier time when either the mountain ranges now separated from one

another were continuous or an intermingling and exchange of species were rendered possible by floral displacements occasioned by vicissitudes of climate. Before the influx of the first Miocene sea through Servia into Hungary and Austria, the Bakonyer Wald were joined to the Southern Limestone Alps; peaks of the height of the Grossglockner lifted their heads where now only low crests surmount the deposits of the Miocene sea, and those lofty peaks were no doubt clothed with an alpine flora. Similarly there was then no lack of high mountains covered with alpine vegetation between the Alps and the Carpathians. Geological information of this character is certainly of great value when it is a question of explaining the close relationships existing between the alpine flora of the Eastern Alps and that of the Carpathians; but the presence of such mountains before the Miocene Period does not suffice to explain the uniformity of the alpine species, the affinity existing between the natural groups to which they belong, and the curious overlapping and interlacing of the boundaries of their areas of distribution on the high mountain ranges which run from west to east and from north to south. There must also have been at that time some impelling cause to account for the intermingling of the floras in question, and for the displacement of their boundaries. The only phenomena which can be presumed to meet the case are alterations of climate of so drastic a nature as to cause a simultaneous descent—and subsequently again a simultaneous return—of the alpine species belonging to the two mountain-chains. These climatic changes must have been the same as those which culminated in the successive formation and advance and subsequent retreat of glaciers in those of the mountains which were lofty enough and of suitable conformation.

In the most widely different strata of our earth's crust, deposits occur which are to all appearance moraine-débris, and are looked upon as glacial deposits by every unbiassed geologist. There is, therefore, good ground for the hypothesis that an alternate advance and retrogression of glaciers has taken place not only in the Diluvial period, but also in the Tertiary period, and generally in all the periods distinguished by geologists. In my opinion the periodical return of a cold, wet climate, manifested in suitable localities by an increase of glaciers, has everywhere and in every age been the cause of migrations, and indirectly of inter-crossing, the formation of new species and the extinction of old ones; and I think that, so far as it goes, it accounts for the displacements, modifications of type, and other changes undergone by the various floras in successive geological periods. Mountains have played an important part in this history. They are able to produce an inexhaustible supply of plants ever ready to colonize less elevated regions down to the plains below, for their slopes are the camping-ground of plants adapted to every kind of climate. When a slight diminution of temperature occurs, the denizens of the lower forest region spread over the plains; a more considerable access of cold impels the plants of the upper forest-region to become the invaders, and so on until it comes to the turn of the vegetation which subsists close to the limit of perpetual snow, where the snow vanishes for only about 50 days each year. And, just as on occasion of a fall in temperature, the plants gradually descend the mountain sides and disperse them-

selves over the lowlands, so also if the temperature rises they are able to retire to the heights again. No more need be said to show that the advance and retreat of vegetation has taken place, and does still take place, *pari passu* with the growth and melting away of glaciers.

Very various notions concerning the cause of the periodical return of an ice-age have prevailed from time to time. Several prominent experts of the present day believe that alterations in the eccentricity of the earth's orbit are the cause of the phenomenon. When the eccentricity increases the earth's surface is considerably cooled, and as the eccentricity diminishes the heat increases. A period of great eccentricity must have begun about 240,000 years before our era and have lasted 16,000 years. Similarly the great eccentricity which existed 850,000 and 2,500,000 years before our era must have brought about repeated glaciation. By others an alteration of the position of the pole is considered to be the cause of the phenomenon in question. Much may no doubt be urged against this explanation, but several phenomena in the plant-world are more easily reconciled with it than with any other. One example of these is the existence of lofty plants with large foliage in the Arctic region during the Miocene, Cretaceous, and Carboniferous periods, as is proved by the discovery of numbers of fossil remains. In the Miocene and Cretaceous periods, Tulip-trees, Magnolias, Limes, Planes, Bread-fruit trees, and Water-lilies flourished in North Greenland, Grinnell Land, Iceland, and Spitzbergen. None of these plants can live there now, for the two following reasons. Firstly, the conditions in respect of solar illumination which obtain there would not permit of their healthy development; and, secondly, there is not sufficient warmth to enable them to grow hardily. Since the most eminent geologists of the day have declared against the idea of the interior of the earth being in a fiery, molten condition it will not do to attribute to that source the high temperature necessary for great Planes, Magnolias, and Bread-fruit trees to flourish in such high latitudes. On the other hand, the presence of large-leaved Angiospermous trees in North Greenland, Grinnell Land, Iceland, and Spitzbergen would be satisfactorily explained if it were assumed that the spot which now forms the North Pole—and with it the whole region now called Arctic—then occupied a different position relatively to the earth's orbit, and consequently received a different amount of light and heat.

As regards the history of plants prior to the Eocene and Cretaceous periods no data are afforded by the investigation of the distribution of living plants, and we are thrown back on the fossil remains derived from those older periods. These are unfortunately comparatively scanty, and they no doubt represent but a small proportion of the species which lived before the Cretaceous period. Two conclusions may, however, clearly be drawn from these remains, viz.: firstly, that no single main division existed at that time which is not still represented at the present day; and, secondly, that some very conspicuous genera of particular groups have died out and been replaced by other genera of the same groups. Specially noticeable in this connection are the tree Club-mosses of the Carboniferous period and the Calamites, species of Horse-tail which must have formed extensive forests in the Carboniferous

periods. The occurrence of these curious Calamites of the Carboniferous period strikes one most when they are found in localities where the ground is now occupied by low herbs, Mosses, and Lichens, and is covered with snow for three-quarters of each year, as is the case in Nova Zembla, Spitzbergen, and Bear Island. In the region of the Alps, too, we encounter spots where this surprising phenomenon is again presented. One of the most remarkable is the upland valley in the Tyrol known as the Gschnitzthal. I have for many years passed the summer months in that valley, and it is there that the greater part of this Natural History of Plants has been written. The house which I occupy stands at an elevation of 1215 metres above the sea-level, and is built upon a diluvial moraine in the middle of the valley. The glaciers which made the moraine have retreated 15 kilometres, and now form the head of the valley. On its débris, dating from the Diluvial period, now grow Firs and Pines, Junipers and Heather, all of which are members of the Baltic Flora. Six hundred metres higher up, arboreal growth ceases and the sides and shoulders of the mountains are clothed alternately with extensive Alpine meadows and scrubs of Alpine Rhododendrons and carpets composed of *Azalea procumbens* and of creeping Dwarf Willows. On the Steinacherjoch, one of the neighbouring ridges, at an elevation of 2200 metres above the sea-level, the ground consists of dark fissured slabs of schist, covered with Lichens and Mosses, and here and there overgrown also by Saxifrages and Primulas. If one of these slabs be split open, the inside is found to bear the impress of giant Calamites and Ferns of the Carboniferous period. What an endless series of changes must the vegetation have undergone since the time when groves of Calamites flourished here. Over and over again has the place wherein they now repose been turned into the bed of a sea wherein were constructed the coral reefs which now surmount the dark ancient schist in the form of pale grey dolomitic peaks. Forest after forest of Coniferous or of Angiospermous trees has spread its shade over the spot for a time and then passed away. Huge tracts of ice have filled the entire valley, and upon the débris of the moraines deposited by the glaciers in their progress now rests a carpet of Primulas, Saxifrages, and Gentians.

> "Ebbe und Flut—so wechselt der Tod und das blühende Leben,
> Blumen pflanzet die Zeit auf das vergessene Grab."

GLOSSARY.

Abscission, the natural cutting off of members by means of a layer of separation.

Absciss-layer, a layer of separation. See above.

Acaulescent, stemless, or apparently so.

Accrescent, applied to the parts connected with the flower, as the calyx, &c., which increase in size after flowering.

Acerosæ, Alex. Braun's term for the Coniferæ.

Achene, a dry indehiscent 1-celled 1-seeded fruit.

Achlamydeous, used of flowering plants which have no calyx or corolla.

Acicular, bristle- or needle-shaped.

Acotyledones, old term (De Jussieu) for non-flowering plants.

Acramphibrya, Endlicher's term for Dicotyledons and Gymnosperms, regarded as plants growing both at the apex and at the sides.

Acrobrya, Endlicher's term for plants growing at the apex only.

Acrocarpous, said of Mosses which produce their fruit (sporogonia) at the tips of their shoots.

Acrodromous. See vol. i. p. 633, fig. 150[1].

Actinomorphic, applied to flowers which may be divided vertically into similar halves through two or more planes.

Aculei, slender, rigid prickles, growing from the bark, as in the Rose.

Adhesion, the union of parts normally separate.

Adnate, congenitally united or grown together.

Adventitious buds, buds produced out of their regular order.

Æcidium, in Uredineæ, a cup-like collection of spores which are budded off from the base of the cup.

Æstivation, the folding of the parts of a flower in the bud.

Aggregate fruit, a fruit formed by the crowding together of distinct carpels; the product of a single gynœceum when that gynœceum is apocarpous.

Aggregation, the condition of extreme activity of the stalk-cells of the tentacles of a Drosera-leaf, resulting from mechanical or chemical stimulation.

Akinetes, in Green Algæ, are single cells of the thallus, whose original walls thicken, and which separate from the rest of the thallus; they correspond to the chlamydospores of Fungi.

Alæ, descriptive term applied to the two lateral members or wings of a papilionaceous corolla.

Albumen, any form of nutritive matter stored within the seed and about the embryo.

Albuminous, containing albumen, as in the seeds of grain, Palms, &c.

Aleurone-grains, grains of nitrogenous food-material frequently stored in the reserve-tissues of seeds.

Alga, a chlorophyll-containing member of the Thallophyta; one of the plants, the best known of which are called Sea-weeds.

Alliance, a group of allied families or orders.

Amentaceous, having aments or catkins; consisting of or resembling a catkin.

Amentum, a catkin. See *Catkin*.

Amœboid movements, constant changes of shape resembling those of the "Proteus animalcule" Amœba.

Amphibious, said of plants such as can live either in the water or in the air.

Amphibrya, Endlicher's term for the Monocotyledons.

Amphicarpium, an archegonium when it persists, after fertilization, as a fruit envelope.

Amphigastria, in Liverworts: certain small scales or leaves on the ventral side of the oophyte generation.

Amphigonium, used sometimes by Kerner as a synonym for archegonium.

Amplexicaul, nearly surrounding or clasping the stem: used of the leaf base in certain cases.

Amylum, starch.

Anaphyte, an old term of the nature-philosophers by which the potential independence of every branch or shoot was indicated.

Anastomose, to inosculate or run into each other; to communicate with each other like arteries and veins.

Anatomy, the intimate structure of plants.

Anatropous, said of that form of ovule in which, although the nucellus is straight, the micropyle is bent down to the point of attachment of the funicle, and in which the body of the ovule is united to the funicle, which latter structure is known as the raphe.

Andrœcium, the collective term for the stamens of a flower.

Androgonidia, the cells which in Volvox give rise to spermatozoids.

Androspores, name given to the particular zoospores which in Œdogonium give rise to miniature plants, termed dwarf-males.

Anemophilous, applied to flowers whose pollen is conveyed by the agency of wind; having flowers fertilized by wind-borne pollen.

Animalcule, a vague term applied to small motile organisms in water.

Anisogametes, sexual cells, which show a differentiation into male and female.

Annulus, (1) in Agarics: the ring which often remains round the stalk (stipe), and was originally attached to the edge of the pileus; the remains of the *velum partiale*; (2) in the Moss-capsule: the ring of cells which brings about the throwing-off of the operculum; (3) in the Fern-sporangium: a conspicuous row of cells running vertically, obliquely, &c., around the sporangium, by the contraction of which dehiscence takes place.

Anophyta, Endlicher's term for the Muscineæ.

Anther, the polliniferous part of a stamen; the sac or cavity in which the pollen is contained.

Antheridium, a male sexual organ, usually producing motile spermatozoids.

Anthocyanin, a purple sap-pigment frequent in foliage and flowers.

Antholysis, literally a "loosened" flower, *i.e.* a flower in which the various parts have become more or less foliacious, and from which inferences can be drawn as to the morphological nature of the component parts.

Anthophyta, Alex. Braun's name for the Phanerogamia.

Anthoxanthin, the yellow pigment of flowers and fruits.

Antipodal cells, a group of three cells at the chalazal end of the embryo-sac of Angiosperms.

Apetalæ, Dicotyledons destitute of a corolla.

Aplanospore, a non-motile asexual reproductive cell of the Green Algæ.

Apocarpous, said when the carpels of a gynœceum are separate.

Apophysis, a swelling under the base of the theca in some Mosses.

Apothecium, the disc-like receptacle of an Ascomycetous Fungus.

Arbor, a tree.

Arbuscula, a little or dwarf tree.

Archegonium, in the higher Cryptogams the flask-shaped female sexual organ with neck and venter, the latter containing an egg-cell, the former canal-cells.

Archesporium, a cell or group of cells from which spore mother-cells are produced.

Archichlamydeæ, a large group of Dicotyledons, including the old groups Polypetalæ and Incompletæ.

Areolated, marked with little areas; divided into small areas by intersecting lines.

Aril, an investment to a seed which arises after fertilization. It is usually succulent.

Arthrospore, a form of spore produced in the Schizomycetes by the segmentation of the tubes into cells.

Arundinaceous, reed-like.

Ascidiform, like a pitcher; pitcher-shaped.

Ascidium, a pitcher; an appendage somewhat resembling a pitcher. See *Pitcher*.

Ascus, a form of sporangium characteristic of certain Fungi. It is generally tubular and contains eight spores, the ascospores.

Ash, the inorganic residue which is left after a plant has been burned.

Assimilation, as used here, the building of a plant-substance from the nutriment of the environment. Often restricted to the manufacture of carbo-hydrate from carbonic acid and water.

Asyngamic, used of plants which are prevented from intercrossing by the fact of their non-simultaneous periods of flowering. Nearly related species can thus inhabit the same spot without hybrids ever being formed.

"Attire", an archaic term, applied by Grew to the stamens.

Auricle, an ear-shaped appendage.

Autogamy, self-pollination, ultimately self-fertilization.

Autonomous movements, spontaneous; originating from inherent tendency.

Auxospore, the reproductive cell of a Diatom. See vol. ii. p. 626.

Awn, a bristle-like appendage, especially in the glumes of Grasses.

Axis, essentially the stem. The root is also an axis.

Azygospore, term given to the "zygospore" when it is formed parthenogenetically with conjugation.

Bacterium, one of the micro-organisms concerned in putrefaction: a term rather widely applied to any member of the Schizomycetes.

Barbs, the retrorse appendages of bristles, or the teeth on leaf-margins.

Bark, the usually hard outer investment of a perennial stem (or root) which has arisen in connection with a cork-cambium; actually it includes the products of the cork-cambium and whatsoever is external to it.

Basidium, a cell from which spores or conidia are produced by a process of abstriction.

Bast, inner bark; a special tissue: *soft-bast*, the phloem—includes sieve-tubes and other non-hardened phloem-elements; *hard-bast*, the thickened prosenchymatous elements or bast-fibres.

Bastard, a term sometimes given to a hybrid.

Bedeguar, name given to the mossy red galls on the common Wild Rose.

Berry, a fruit the whole pericarp of which is succulent.

Bilabiate, two-lipped.

Bizzaria, a fruit, part Orange, part Citron. See vol. ii. p. 569.

Blendling, a name given to a hybrid arising by the crossing of "races".

Blossom, cf. vol. ii. p. 71.

Brachydodromous, used of leaf-veins. See vol. i. p. 630.

Bract, a leaf subtending a flower.

Bract-scale, the lower member of the duplex scale of the female cone of Pine, Fir, &c.

Break back, a term used by gardeners to convey the idea of reversion. Thus flowers break back or revert to an ancestral type.

Bud, the as yet unexpanded rudiment of a shoot; it comprehends both axial and foliar portions.

Bulb (bulbus), a bud consisting of an abbreviated axis with fleshy scale-leaves in which food-material is stored. Usually subterranean.

Bulbil, a deciduous bud, usually formed on an aërial part of a plant. Occasionally used for a little bulb.

Callus, the healing tissue which closes up the wounds of plants. The same term is given to a mucilaginous substance which arises on the sieve-plates of the sieve-tubes, closing them. The latter is of course quite a different structure, and to distinguish it from the former may be called *callose*.

Calyptra, the hood which is raised up on the sporogonium of a Moss. It is the ruptured upper portion of the archegonium.

Calyx, the outer whorl of the perianth, consisting of sepals.

Cambiform cells, cells resembling cambium cells: thin-walled, tapering cells found in the phloem accompanying the sieve-tubes, companion-cells, and bast-fibres.

Cambium, a layer of tissue formed between the wood and the bark, and consisting partly of nascent wood, partly of nascent bark.

Campylodromous, applied to the manner in which veins are distributed. See vol. i. p. 633, fig. 150[3].

Campylotropous, used of an ovule or seed in which the nucellus, with its integuments, is bent so that the apex is brought near to the point of attachment.

Canker, a vague term applied to the disease or Fungus which attacks plants and causes slow decay.

Capillitium, the thread-like fibres, often united into a reticulum, which are developed within the spores of Myxomycetes and many Gasteromycetes.

Capitulum, a head or globular cluster of sessile flowers.

Caprification, the custom of hanging branches of the wild Fig in the cultivated trees so as to ensure pollination by means of the gall-insects thus introduced.

Caprificus, the uncultivated male form of the common Fig.

Capsule, a dry, dehiscent fruit.

Carobe di Giude, Turpentine Gall-apple, produced on Pistacia Lentiscus by a Pemphigus.

Carpel, a single-celled ovary or seed-vessel, or a single cell of an ovary or seed-vessel together with what belongs to that cell; it may be regarded as a modified leaf.

Carpium, or **Carp**, the oogonium modified by fertilization, which remains as an envelope around the embryo. Cf. vol. ii. p. 47.

Carpo-asci, the more complex Ascomycetous Fungi —all except the Exoascaceæ.

Carpophylla, the carpels.

Caruncle, a localized outgrowth of the seed-coat; a sort of aril.

Caryophyllaceous, appertaining to the Pink family.

Caryopsis, an indehiscent one-seeded fruit, in which the thin seed-coat adheres to the pericarp, as in all cereal grains.

Catapult-fruits, fruits in which the dispersal of the seeds or fruit-segments is due to the elastic reaction of the resilient peduncles or pedicels.

Catkin, a pendulous inflorescence bearing flowers of one sex only; an amentum.

Caudex, a trunk or unbranched stem.

Caudex columnaris, an erect columnar stem, as in Palm-trees.

Caulescent, having an obvious stem rising above the ground.

Cauline, appertaining to the stem.

Caulis, the stem or stalk.

Caulis herbaceus, a herbaceous stem.

Caulis suffruticosus, a suffruticose stem; the stem of an under-shrub.

Caulome, a stem-structure, or the stem-like portion of a plant.

Cecidium, a gall or hypertrophy on a plant-member, due to the stimulating action of an insect or Fungus.

Cell, the structural unit in the formation of plants; one of the individualized portions of which plants are built up.

Cell-membrane, the cell-wall.

Cell-plate, used here of aggregates of cells in one plane.

Cell-sap, the watery fluid contained in a cell.

Cellular, consisting of cells. Sometimes used of plants which are destitute of vessels.

Cellulose, a carbo-hydrate of which cell-membranes are composed; the essential constituent of cell-walls.

Centrifugal, a term applied to such inflorescences as develop from the centre outwards.

Centripetal, a term applied to such inflorescences as develop from without inwards.

Cephalonion gall, a sac-like gall joined to the leaf by a narrow neck.

Ceratonion gall, a hollow, thick-walled, horn-like gall, belonging to the series of Mantle-galls.

Chalaza, the part of an ovule where nucellus and integuments cohere; the base of the nucellus.

Chalazogamic, applied to fertilization in flowering plants via the chalaza and not by the micropyle, *e.g.* in the Hazel.

Chlamydospore, the reproductive organ in some Fungi.

Chloranthy, the production of green flowers; a supposed reversion of floral structures to a primitive foliar condition.

Chlorenchyma, a term sometimes given to a green, chlorophyll-containing tissue.

Chlorophyll, the ordinary green pigment of plants which is the agent in the process of carbon assimilation.

Chlorophyll-corpuscles, protoplasmic bodies distinct from, yet imbedded in, the general cell-protoplasm of the green parts of plants. The chlorophyll is restricted to these corpuscles.

Chromatophore, a general term for any protoplasmic body containing a pigment. Chlorophyll-corpuscles are chromatophores.

Chromosomes. See *Fibrils*.

Cilia, delicate protoplasmic filaments serving as organs of locomotion, as in zoospores, &c.

Cincinnus, a form of cymose inflorescence, a one-sided cyme.

Cirrhus capreolus, a term for stem-tendrils, *i.e.* branch-tendrils and flower-stalk tendrils.

Cirrhus costalis, a projecting or excurrent midrib, modified as a tendril.

Cirrhus foliaris, a leaf modified as a tendril.

Cirrhus peduncularis, a flower-stalk modified as a tendril.

Cirrhus petiolaris, a petiole or leaf-stalk modified as a tendril.

Cirrhus radicalis, a root modified as a tendril.

Cirrhus rameaneus, a tendril which is a modified branch.

Cirrhus stipularis, a tendril which is a metamorphosed stipule.

Cladodes, leaf-like branches. See *Phylloclade*.

Clamp-cells, here used for the papilla-like cells by which an epiphytic root adheres to the substratum.

Class, the highest grade or division of plants in the system of Linnæus. In our system a class is subordinate to a phylum, and the classes are subdivided into alliances.

Clavate, club-shaped.

Claw, a name given to the stalk of a petal.

Cleistogamic, -ous, a term applied to the inconspicuous flowers produced by many plants. These flowers do not open, and are self-pollinated (autogamous).

Cob, a term applied to the spike on which Maize grows.

Cœnobe, or **Cœnobium**, a colony of separate organisms united by a common investment, *e.g.* Volvox.

Coherent, used of the union of similar members.

Cohort, a group of families or orders which are nearly related to one another; is used here as synonymous with Alliance.

Collective fruit, a fruit in which the products of a number of *separate* flowers become so crowded together as to appear as though they had arisen from a single flower, as the Pine-apple. Cf. *Aggregate fruit*.

Collenchyma, a living tissue, consisting of prism-shaped cells whose angles are much thickened. It is a form of mechanical tissue.

Colony. See vol. i. p. 585.

Columella, in Muscineæ, the sterile tissue in the centre of the sporogonium around which the spore-layer is formed.

Column, the body formed as a result of fusion of stamens with style, as in Orchid flowers.

Conceptacle, the inclosing cavity in which the sexual organs are produced in the Fucaceæ.

Cone, the aggregate of crowded scales which bear ovules or pollen-sacs in the Gymnosperms; applied also to the sporangiferous branches in many Vascular Cryptogams.

Conidium, in Fungi, a propagative asexual body.

Conifer, a plant producing cones; one of the Coniferæ.

Conjugation, the union of two gametes (or sexual cells), the resulting organism being called a *zygote*.

Conjugation-canal, the bridge which is formed between conjugating cells of Spirogyra, &c., and by which impregnation is effected.

Connate, united congenitally.

Conopodium, a conical receptacle (used of flowers).

Contorted æstivation, used when the corolla appears spirally twisted, the petals being so arranged that one margin is external to a neighbouring petal whilst the other is internal to the petal on the other side.

Contractile cells, in the anther, form a layer in its wall; their membranes are peculiarly thickened, and by their hygroscopic contractions the anther opens.

Convolute, applied to a leaf which is rolled up longitudinally in the bud.

Cordate, heart-shaped, as a leaf.

Corm, a bulb-like fleshy stem or base of a stem; a "solid bulb", as in Crocus, Colchicum, &c.

Cormus. See foot-note, vol. i. p. 665.

Corolla, the inner whorl of the perianth, composed of petals.

Corona, in Narcissus, &c., a series of ligular structures on petals, which may be either free or united together. It gives the appearance of an additional floral whorl.

Corpuscle, a little mass of protoplasm which though imbedded in the general protoplasm of the cell is nevertheless an independent body, *e.g.* chlorophyll-corpuscle.

Corpusculum (of Asclepiad pollinium), the little body connecting the pollen-masses and by means of which they become attached to insects.

Cortex, the portion of a stem or root external to the vascular tissues.

Corymbus, or **Corymb**, a flat-topped inflorescence belonging to the centripetal or indefinite series.

Cosmic dust, the minutely divided inorganic particles suspended in the higher strata of the atmosphere; not necessarily of extra-terrestrial origin.

Cosmopolitan plants are such as range almost over the entire globe; in contrast to plants that flourish only in a certain locality (*endemic* plants).

Cotyledons, seed-leaves; the first leaf or leaves of an embryo.

Craspedromous, used of the lateral veins of a leaf which run undivided from midrib to margin.

Crateriform, goblet- or cup-shaped.

Crenate, said of a toothed leaf-margin, the teeth being rounded; scalloped.

Cross-fertilization, the fertilization of an egg-cell by a male cell borne on another individual; fertilization of the ovules of one flower by the pollen from another individual. Occasionally used in error in the text for cross-pollination (which see). Many authors use the term as synonymous with cross-pollination, but the practice is not good.

Cross-pollination, the deposition on a stigma of pollen which has been brought from another flower. Cross-pollination, though probably leading to cross-fertilization, is not synonymous with this term.

Cruciferous, "cross-bearing", having cross-shaped flowers: used of the characteristically flowered family Cruciferæ.

Cryptogamia, includes all plants exclusive of Flowering Plants: opposed to *Phanerogamia*. An old term, persisting from times when the reproductive processes of these plants were less well-known than to-day.

Crystalloid, a crystal-like mass of proteid; a common form under which proteids are stored.

Culmus, or **Culm**, the jointed and usually hollow stem of Grasses and similar plants.

Cupule, the bract-like cup which incloses the nut or nuts in many Amentiferæ; it is the husk of the hazel-nut, the cup of the acorn, the prickly envelope of the Spanish chestnut, &c.

Cut, a term applied to the lobing of leaf-blades; incised; cleft.

Cuticle, a continuous film on the surface of a plant, formed of the cutinized outer surfaces of the epidermal cells.

Cyma, or **Cyme**, a definite or centrifugal inflorescence: the laterals grow more strongly than the primary axis and overtop it.

Cyma composita, or compound cyme; a definite or centrifugal inflorescence, in which the ultimate parts (cymes) are also arranged in a cymose manner.

Cystolith, a concretion of carbonate of lime, generally deposited on a little tongue or peg of cellulose projecting into the cells of certain plants.

Cytoplasm, the protoplasmic body of a cell as opposed to the nucleus.

Daughter-cells, cells which arise by the division of any cell.

Deciduous, non-permanent: used of parts of a flower (petals, &c.) which fall after flowering, and of leaves which fall in autumn, &c.

Decurrent, used of leaf-blades which have their bases extending downward along the stem.

Decussate, applied to leaves which are arranged in pairs alternately crossing each other at regular angles.

Definitive nucleus, the nucleus which is formed in the embryo-sac by the fusion of two, one from each end; the endosperm originates from it after fertilization has taken place.

Dehiscence, the act or mode of opening of a fruit, anther, spore-capsule, &c. &c.

Dendritic, tree-like; repeatedly branched.

Denizen, an inhabitant, a plant belonging to a certain district. Strictly (but not so used in K. and

O.), a plant resembling a native, but suspected of having been originally introduced.

Dentate, of leaf margins; toothed—the teeth pointing *outwards*, not forwards or backwards.

Dermatogen, the embryonic cellular layer at the apex of a stem or root from which the epidermis is developed.

Desmid, one of the Conjugatæ. See vol. ii. p. 655.

Dextrorse, used of twining plants which turn from west through south to east, &c.

Diadromous, having a fan-like arrangement of leaf-veins, as in Gingko.

Dialypetalæ, plants with petals separate from one another (= Polypetalæ).

Diandria, the 2nd class of Linnean system; includes all genera with perfect flowers having two stamens.

Diastase, a solid, white, soluble substance found in Oats, Potatoes, &c., after germination.

Diastole, used of the rhythmic expansion of a contractile cell or vacuole.

Diatom, a single organism inclosed in a bivalved siliceous test or frustule. See vol. ii. p. 625.

Diatomin, the brown pigment of Diatoms.

Dichogamy, the maturing of pollen and stigma in a hermaphrodite flower at different times, to prevent self-fertilization.

Dicotyledon, plant with two seed-leaves or cotyledons.

Dictyodromous, or reticulate venation, are terms applied to lateral veins of leaves which break up into a network before reaching the margin.

Didynamia, the 14th class of the Linnean system, which includes flowers with four stamens, two long and two short.

Didynamous, applied to flowers having four stamens, one pair longer than the other.

Dicœcious, unisexual; the male and female flowers being on separate plants.

Diosmosis, the transfusion of a fluid through imperceptible openings in a membrane.

Diptero-cecidia, gall-structures, due to dipterous insects.

Discoid, resembling a disc.

Discomycete, any Fungus belonging to the group Discomycetes, *i.e.* an Ascomycete in which the fruiting body is disc-shaped.

Discomycetous, pertaining to the group of Fungi Discomycetes.

Discopodium, a disc-shaped floral receptacle.

Disintegration, a resolution of a tissue into its constituent cells, or of any body into its constituents.

Displacement, in whorls, applied to the shifting of places of insertion of members, so that successive whorls are placed immediately above one another.

Divergence, applied to the angle between the insertions of successive leaves on a stem.

Divided, used of leaf-blades to express the fact that they are deeply lobed.

Dormant eyes or buds, or **Reserve-buds**; are buds which arise in the leaf-axils in the usual way, but which do not forthwith expand into shoots; they remain—often many years—until stimulated into activity by some special event.

Drupaceous, of the nature of a drupe.

Drupe, a succulent fruit with hard, stony endocarp, which incloses a single seed. Many-seeded drupes are rare.

Duct, a continuous tube, arising either by the running together of cells (fusion), or by the separation of cells, when it is lacunar in nature; a canal formed by a row of cells having lost their partitions.

Dwarf-male, of Œdogonium; the little few-celled plant arising from an androspore which gives rise to the spermatozoids. It is formed adjacent to the oogonium.

Ectoplasm, the pellicle-like outmost layer of protoplasm in a cell. It is clear and hyaline, and less fluid than the endoplasm.

Egg-cell, or **Ovum**; the female generative cell.

Elaters, (1) in Liverworts, filamentous cells, with spiral thickenings, which are present with the spores, and, owing to their hygroscopicity, assist in their dispersal; (2) in Equisetum, arm-like appendages of the spores, by the contractility of which the spores become entangled in groups.

Ellipsoidal, having the form of an elliptical solid.

Embryo, the rudimentary plant; in seeds, that stage of the young plantlet at which the resting-stage supervenes.

Embryo-cell, the cell borne at the distal end of the suspensor, which gives rise to the embryo, or to the greater part of it.

Embryo-sac, the large cell in the nucellus of an ovule, in which the egg-cell, and ultimately the embryo, arises.

Endemic, restricted to a given region or locality.

Endophytic, living within the tissues of another plant, though not necessarily parasitic upon them.

Endoplasm, the soft, inner granular protoplasm of a cell.

Endosmosis, the transmission of fluids through porous membranes from the exterior to the interior.

Endosperm, the tissue produced within the embryo-sac of flowering plants, and which in many cases becomes stored with food-materials for the embryo.

Endospores, asexual reproductive cells produced inside the original cells in Bacteria.

Endothecium, in flowering plants, the layers of the wall of the anther internal to the exothecium.

Ennobling, the art of transferring a branch or bud of one plant to another, and causing them to unite.

Entire, untoothed: applied to the leaf-margin, petals, &c.

Entomophilous plants, such as have flowers pollinated by insect agency.

Enzyme, any of the unorganized ferments which exist in seeds, as diastase, pepsin, &c.

Ephemeral, applied to flowers which endure only for a few hours or for a day; opening but once.

Epicotyl, the portion of a plant above the cotyledons; restricted to embryos and seedlings.

Epidermis, that layer of cells which forms the enveloping mantle of multicellular plant-bodies. It may be replaced in perennial plants by cork.

Epigeal, growing above the ground.

Epiphragm, of Mosses: the membrane remaining after the fall of the operculum, stretched across the mouth of the capsule in Polytrichaceæ.

Epiphyllous, applied to structures growing on leaves.

Epiphytes, plants growing attached to other plants (or animals), but not parasitically.

Equitant, riding; folded around, as if straddling over.

Erythrophyll, a red sap-pigment frequent in foliage-leaves, especially in autumn.

Ethereal oils, oils of wide occurrence in plants, and of various chemical composition; to the presence of these ethereal or volatile oils are due most of the odours of plants.

Evolute, turned back.

Exalbuminous, applied to seeds which are destitute of endosperm or perisperm, the food-material being stored in the embryo itself.

Excoriation, of glandular hairs; applied to the act of throwing off the cuticle as a blister.

Exfoliate, to come away in scales or flakes, as the bark of a tree.

Exine. See *Extine.*

Exogamy, the tendency often exhibited by closely related gametes to avoid pairing.

Exosmosis, the passage from within outwards of fluids through a membrane.

Exothecium, the outmost layer or epidermis of an anther.

Exstipulate, without stipules: often used (though erroneously) in cases where the stipules are early deciduous.

Extine, the outer coat or membrane-layer of a pollen-grain. It is, however, internal to the perine.

Extravasation, an escape from the proper vessels into surrounding tissues: used of fluids.

Extrorse, applied to such anthers as open towards the outer whorls of a flower, *i.e.* away from the gynœceum.

Eye, of Potato, &c.; an undeveloped bud.

Eye-spot, in motile gametes and spermatozoids, a little red pigment-body contained usually in the anterior extremity, and supposed to be sensitive to light. Cf. vol. ii. p. 629.

Fairy-ring, a phenomenon observed in meadows, and due to the growth of certain Fungi. Cf. vol. ii. p. 792.

Fasciation, used of monstrous expansions of stems, which resemble several stems fused together in one plane.

Fascicula, or **Fascicle**, a dense cluster of flowers, leaves, roots, &c.

Father-plant, the stock from which the pollen is derived: used in connection with hybrids.

Ferment, a substance produced by the protoplasm, which induces chemical change or fermentation in some substance without itself entering into or being affected by the process.

Fertilization, the process by which the pollen reaches and acts upon the ovules, and results in the production of fruit; impregnation.

Fertilizing-tube, in Peronospora, the tubular outgrowth of the antheridium which penetrates the oogonial wall and by which the male substance passes to the egg-cell.

Fibre, any delicate filament; also, a thick-walled tapering cell.

Fibrils of nucleus; the segments into which the nuclear reticulum breaks up at division; they are also termed *chromosomes.*

Fibrous layer, of anther: the specially thickened portion of the wall which brings about dehiscence.

Filament, the stalk of an anther.

Filiform, slender, thread-like.

Fimbriate, fringed by fine subdivision of the margin; having fine, hair-like marginal processes.

Fistular, hollow, reed-like.

Flagellum, the whip-like process or filament of protoplasm which serves as an organ of motility; also a shoot sent out from the bottom of a stem, as in the strawberry; a runner.

Floccose, composed of or bearing soft hairs or wool.

Flora, the aggregate of the plant-population of any district; also, the term given to a systematic description of the same.

Floral, belonging to the flower.

Floret, a small flower in a cluster or in a compact inflorescence, as in the Compositæ.

Flower, in Phanerogams the growth which comprises the reproductive organs and their envelopes; a shoot modified for the production of spores (pollen-grains and embryo-sacs).

Flowering glume, the outer of the two chaffy scales inclosing the several flowers of a grass; it is frequently awned.

Folium fulcrans, the subtending leaf of a flower; a bract.

Follicle, a monocarpellary dehiscent fruit opening only down the ventral suture.

Foot, the sucker by means of which a young Fern-plant is temporarily attached to the prothallium.

Foreign, applied to pollen from another flower.

Frugivora, animals which live upon fruits.

Fruit, defined vol. ii. p. 47.

Frustule, the siliceous valve of a Diatom.

Frutex, a shrub.

Fruticose, pertaining to shrubs; shrubby.

Fruticulus, a little shrub.

Fuliginous, having the colour of soot.

Fundamentum, the hypocotyl, which see.

Fungus, a cellular Cryptogam, distinguished for its want of chlorophyll; it is either saprophytic or parasitic.

Funicle, the stalk of an ovule or seed; a funiculus.

Furfuraceous, scurfy; covered with bran-like scales.

Fusiform, spindle-shaped: applied to roots, &c., which taper both ways from the middle, as the radish.

Galeate, helmet-shaped; having a galea or helmet.

Gall, a vegetable excrescence produced by the deposit of the egg of an insect in the bark or leaves of a plant; a hypertrophied growth due to some irritating cause.

Gametangia, cells from which gametes are developed.

Gamete, a sexual cell.

Geitonogamy, crossing between separate flowers growing on the same plant.

Gemma, a small undeveloped shoot; a shoot-bud.

Gemmation, the act or process of budding.

Generative cell, in pollen-grains, that cell which ultimately fertilizes the egg-cell.

Genetic spiral, the spiral line passing through the point of insertion of equivalent lateral members (leaves) on an axis in order of age from older to younger.

Genus, an assemblage of species; its name, together with that of the species, gives the name to the plant.

Geotropism, applied to the power or tendency of some plants to grow towards the earth.

Germen, the ovary.

Germination, the act, process, or result of evolving the embryo of a seed into a young plant.

Gills, the radiating plates on which the basidiospores of Agarics are produced.

Glabrous, without hairs; quite smooth.

Glandular, having the nature of a gland, bearing glands.

Gleba, the chambered, sporogenous layer of a Gasteromycetous Fungus.

Globoid, the tiny mass of magnesium and calcium phosphate which is often present in aleurone grains (which see).

Glomerule, a cymose inflorescence formed into a head, as in the Globe-thistle.

Glucoside, a compound consisting of glucose and an aromatic body.

Glumes, the chaffy, bract-like scales on the inflorescences of Grasses and Sedges.

Goneoclinic, used of hybrids which approximate to one or other parent-form rather than standing midway between them.

Graft-hybrid, a hybrid supposed to have arisen by budding or grafting.

Gynandria, the 20th class of the Linnean system. Cf. vol. ii. p. 290.

Gynœceum, the carpel, or aggregate of carpels, in a flower; the female portion of a flower as a whole.

Habitat, the natural abode of a plant.

Hæmatochrome, the red pigment found in the eyespots of Chlamydomonadeæ and zoospores.

Halophytes, plants which flourish on soils rich in salt; saltworts.

Haulm, the stalk of a grass of any kind.

Haustorium, the sucker of a parasitic plant.

Herbaceous, of the colour, texture, &c., of a herb.

Herbal, a book of descriptions of plants with especial reference to their medicinal properties; herbals were usually copiously illustrated.

Herbarium, a collection of dried plants systematically arranged. (Formerly it signified an illustrated herbal.)

Hermaphrodite, applied to a flower which has both stamens and carpels.

Heterochromatism. *Vide* vol. ii. p. 569.

Heterœcism, the act of passing through different stages of development on different hosts; as in Fungi.

Heterogamous, applied to plants that bear two kinds of flowers which differ sexually.

Heterogamy, the state or quality of being heterogamous (which see); cross-pollination.

Heteromorphism, here used to designate the various modifications of equivalent members in connection with different functions, analogous to that existing among the polyps of a coral.

Heterophyllous, bearing leaves of more than one form on the same stem; applied especially in respect of foliage-leaves.

Heterosporous, having spores of different kinds, especially macrospores and microspores.

Heterostyled, when the flowers of a plant differ in the relative length of their styles: opposed to *homostyled*.

Hilum, (1) of starch-grain; the centre around which the stratifications are deposited; (2) of a seed; the scar or place of attachment.

Hirsute, bearing rather stiff hairs.

Holosericeus, covered with fine silky hairs.

Homochromatism. *Vide* vol. ii. p. 569.

Homosporous, having spores all of a kind.

Homostyled. See *Heterostyled*.

Hortus vivus, an old term for a dried collection of plants, now called a *herbarium* (*hortus siccus* is also used in the same sense).

Humus, vegetable mould; a soil largely composed of decaying vegetable matter.

Hybrid, a plant resulting from the intercrossing of more than one species.

Hybridization, the act of crossing different species and so producing hybrids.

Hydrophytes, plants which live in water.

Hydrotropism, the particular irritability of plant-members (especially roots) whereby they respond by curvatures to moisture in the environment, turning towards or away from it.

Hymenium, hymenial layer; the spore-bearing surface of a fungal receptacle.

Hypanthium, a term given to any special enlargement of the receptacle, as in the Rose.

Hypha, the filamentous element of the thallus of a Fungus.

Hyphodromous, used when the veins of a leaf run so that they are not visible on the surface.

Hypocotyl, the portion of the stem below the cotyledons.

Hypocrateriform, salver-shaped: used of corollas, &c., which are tubular below and suddenly expand into a flat limb.

Hypogeal, underground; growing beneath the surface of the earth.

Hysterophyta, Endlicher's term for the parasitic flowering plants.

Idioplasm, name applied by Nægeli to that portion of the protoplasm in which the formative activity was supposed to reside — the active, organizing portions of the protoplasm.

Illegitimate union in heterostyled flowers. *Vide* vol. ii. p. 405.

Imbricate æstivation. *Vide* vol. ii. p. 210.

Imbricating, overlapping like the tiles of a roof.

Incised, of leaves, cut irregularly and sharply.

Indumentum, a hairy covering or coating.

Indusium, the scale-like outgrowth of a Fern leaf enveloping the sorus.

Inferior, (1) of the ovary; adherent to the calyx (cf. also vol. ii. p. 79); (2) of the calyx, free from the ovary; (3) in regard to the relation of parts of flower to the axis; farthest from the axis.

Inflorescence, the mode of branching of the flower-bearing part of a plant; or, the actual cluster of flowers (the common use of the term).

Infundibuliform, Infundibular, funnel-shaped.

Innovatio, a new-formed shoot.

Insectivorous plants, plants which catch insects and absorb their juices.

Integument, the envelope—single or double—of an ovule.

Internode, the portion of a stem between the points of insertion of leaves.

Intine, the internal layer of the wall of a pollen-grain.

Introrse, of the anther; dehiscing towards the centre of the flower.

Intussusception, the taking up by a living organism of new particles between those already in existence.

Invertin, a ferment which converts cane-sugar into glucose.

Involucral, appertaining to the involucre.

Involucre, a circle of bracts inclosing a capitulum or other crowded inflorescence.

Involute, rolled inward.

Isogametes, equivalent gametes or sexual cells.

Isoplanogametes, in Algæ; motile sexual cells which are equal in size.

Kamptodromous. See vol. i. p. 630.

Labellum, the median member of the inner perianth-whorl in Orchids.

Laciniated, cut into narrow lobes.

Lacuna, a space, especially an intercellular space, originating by the separation or breaking down of cells.

Lamella, a thin plate as in the gills of Agarics. See *Gills*.

Lanceolate, shaped like a lance-head; narrower than oblong, and tapering towards the apex.

Latex, plant juice, often a milky juice.

Laticiferous, containing latex.

Leaf-axil, the angle formed by a leaf and the portion of stem immediately above its point of insertion.

Leaves, laterally-developed members of limited growth, which spring in geometrical succession from the outer layers of tissue below the growing point of the stem.

Legitimate union, in heterostyled flowers. *Vide* vol. ii. p. 405.

Legume, or **Pod**; a monocarpellary fruit dehiscing down both sutures.

Lepidote, **-us**, beset with scurfy scales.

Liane, **Liana**, a climbing plant with a woody, perennial stem.

Libriform cells, strong, spindle-shaped cells with inconspicuous pittings, thick walls, and usually destitute of protoplasmic contents. They occur in wood.

Lichen, an organism compounded of a Fungus and an Alga living together symbiotically.

Lignin, an aromatic substance (or number of substances) present in the membrane of woody tissue. To it are due the characteristic properties of wood.

Ligulate, provided with a ligule.

Ligule, **Ligula**, (1) the thin scarious projection from the summit of the leaf-sheath in Grasses; (2) the corolla of a ray-floret in the Compositæ; (3) a tongue-like outgrowth on the leaf met with in Selaginella and Isoëtes just above the insertion of the sporangium.

Linear, several times narrower than long, with the margins parallel.

Linear-lanceolate, intermediate in form between linear and lanceolate.

Lines of vegetation, for any species, are the lines obtained by joining all the places in a given direction at which that species is checked in its distribution by climatic or other conditions; the resultant figure obtained by joining all the lines of vegetation covers the distribution of the species in question, and may be termed the line of distribution.

Lithophytes, plants which grow on stones, and derive their nutriment in the main from the atmosphere.

Liverwort, a term applied to any member of the Hepaticæ.

Lobe, any division of an organ; a rounded projection or division.

Lodicules, tiny scales, usually two in number, which occur in the flowers of Grasses, and are supposed to represent the perianth.

Lomentum, a legume which separates into 1-seeded articulations or joints.

Macropodous, applied to embryos in which the hypocotyl is enormously enlarged, constituting the greater part of the embryo.

Macrospores, used of the larger (so-called female) spores of heterosporous plants: opposed to *microspores*.

Manubrium, the cell in the antheridium of Characeæ which projects inwards from the shield, and ultimately bears the antheridial filaments.

Medulla, pith.

Megagametes, used of the larger, and presumably female, motile sexual cells of certain Algæ.

Melliferous, honey-bearing.

Mericarp, one of the achene-like fragments into which a syncarpous, polycarpellary fruit (schizocarp) breaks up. Used especially of Umbelliferæ.

Meristem, embryonic tissue: growing cell tissue at the ends of young stems, roots, &c.

Mesophyll; the whole of the internal ground-tissue of a leaf-blade.

Metabolism, the chemical changes which take place in the protoplasm and which it causes in other substances; the phenomena resulting from chemical changes in the protoplasm.

Micellæ, name given to molecular aggregates, just as molecule is the name given to atomic aggregates.

Microgametes, used of the smaller, presumably male, motile sexual cells of certain Algæ.

Micro-millimeter (μ), the one-thousandth part of a millimeter.

Micropyle, the aperture left in the integument of an ovule by means of which the pollen-tube gains access (except in chalazogamic plants) to the embryo-sac.

Microsomata, tiny granules of various nature embedded in the protoplasm. Not a good term.

Microspores, the smaller or so-called male spores of heterosporous plants: opposed to *macrospores*.

Midrib, the central or main vascular bundle of a leaf.

Monadelphous, when the stamens are all united together by their filaments into a tube or column.

Monandria, the 1st class of the Linnean system. See vol. ii. p. 288.

Moniliform, like a necklace or string of beads.

Monocarpellary, consisting of one carpel.

Monocotyledonous, having only a single cotyledon or seed-leaf.

Monœcia, the 21st class of the Linnean system. See vol. ii. p. 290.

Monœcious, having male and female flowers on the same individual.

Monotypic, term used of genera which comprehend but a single species, *e.g.* Welwitschia.

Morphology, that department of botanical study which deals with the form of the plant-body, including its development, the growth of its distinct members, &c.

Mother-plant, that parent of a hybrid upon which the seed is matured.

Mycelium, the filamentous vegetative body of a Fungus.

Myco-cecidium, a gall which owes its origin to the attacks of Fungi.

Mycorhiza, a root invested by a fungal mantle: supposed to be a case of symbiosis.

Mycosis, a diseased condition of animal tissues alleged to be due to the presence of a Mould-fungus.

Myrmecophilous, used of plants which attract ants, the latter often living altogether upon the plant and affording it protection against certain enemies.

Nectary, a honey-secreting gland or part of a flower.

Neroli, Oil of, the ethereal oil yielded by the flowers of the Orange-tree.

Neuter flowers, flowers destitute of functional stamens or carpels.

Node, the part of a stem at which a leaf or whorl of leaves is inserted.

Nodose, or **Nodosus**, knotty; having well-marked nodes or knots.

Nodulated, having small knots: diminutive of *nodose*.

Nucellus, the central portion or body of an ovule, containing the embryo-sac.

Nuclear plate, the assemblage of nuclear fibrils in the equator of a nucleus during the division of the latter.

Nucleus, (1) of starch-grain, same as hilum; (2) of an ovule, an old term for *nucellus*; (3) the cell-nucleus, a specialized portion of the protoplasm of a cell exhibiting remarkable figures during division and presiding over the chemical processes that take place in the cell.

Nut, a hard, indehiscent, 1-seeded fruit resulting from a polycarpellary ovary.

Nutation, spontaneous changes in position of growing organs; a kind of oscillation or regular movement in parts of plants.

Obovate, ovate with the broader end at the apex.

Omphalodium, the scar at the hilum of a seed.

Ontogeny, the history of the individual development of an organized being.

Oogonium, the cell in which the female sexual cell or cells are produced; especially amongst Thallophytes.

Oophyte, that stage in the life-cycle of a plant which bears the sexual organs.

Ooplasm, the substance of which the female sexual cell consists. Not a good term.

Ooplast, the female sexual cell. Not a very good term.

Oospore, a fertilized egg-cell.

Operculum, the lid of a Moss capsule.

Order, a division of plants intermediate between class and genus, consisting usually of a group of genera related to one another by structural characters common to all. Same as *family* as used in this book.

Orthostichies, vertical ranks of leaves. Cf. vol. i. p. 397.

Orthotropous, applied to an ovule with straight nucellus wherein the micropyle is at a point far removed from the funicle.

Osmosis, the tendency of fluids to pass through porous membranes; the phenomena attending the passage of fluids through porous membranes.

Ostiole, the aperture of the conceptacle in the Fucaceæ.

Ovary, the part of the pistil that contains the ovules or immature seeds; the closed chamber-like portion of a single free carpel, or the many chambers of several united carpels in which the ovules are produced.

Ovule, in Phanerogams is the macrosporangium or nucellus with its integuments, and containing the embryo-sac. The ovule is the immature seed.

Ovuliferous scale, the ovule-bearing scale of Conifers.

Palæo-botany, Fossil botany.

Palate, a projection in the throat of a personate corolla (or corolla such as that of the Snapdragon).

Palea, the inmost of the glumes which inclose the individual flowers of Grasses; a chaffy scale or chaff-like bract.

Palisade-cells, the green assimilating tissue, consisting of cylindrical cells, usually found towards the upper surface of the leaf-blade.

Palmate (of leaf-blades), lobed so that the projections radiate from the point of insertion.

Panicle, a loose branched cluster of flowers. Not applied very strictly.

Papilionaceous, like a butterfly: a term applied to the corolla of a section of Leguminosæ, including the Pea and Bean, &c.

Papilla, a minute nipple-shaped projection.

Papillose, bearing papillæ.

Pappus, the hairy or feathery development of the calyx of a Composite plant, which promotes dispersal by wind; thistle-down or the like.

Parallelodromous. See vol. i. p. 634.

Paraphyses, sterile filaments accompanying the sexual organs in Mosses, the asci and basidia of Basidiomycetes, and in other cases.

Parasite, a plant which lives upon and obtains organic nutriment from the tissues of a living plant (or animal).

Parastichies, secondary spirals in the arrangement of leaves.

Parenchyma, usually thin-walled tissue consisting of cubical or polygonal cells, and forming the pulp of leaves, fruits, &c.

Parthenogenesis, the development of an egg-cell into an embryo without fertilization taking place.

Parthenogonidia, certain reproductive cells in a Volvox-colony which propagate the plant asexually.

Partite, cleft, but not quite to the base.

Patelliform, disc-shaped; circular with a rim.

Pedate venation. See vol. i. p. 633.

Pedicel, an ultimate flower-stalk bearing a single flower.

Pedunculus, or **Peduncle**, a general flower-stalk bearing either a single flower or a closely-crowded cluster of flowers.

Peltate, shield-like: said of leaves when the petiole is attached to the under surface of the blade and not to the margin.

Perfoliate, appearing as if perforated by a stem: said where a stem is so embraced by a leaf that the former seems to pass through the latter.

Perianth, the floral envelopes, consisting of calyx or corolla, or both: used especially when it is not easy to distinguish between them.

Periblem, the embryonic tissue at a growing point from which the primary cortex arises.

Pericarp, -ium, the wall of an ovary that is developed into a fruit.

Perichætium, the sheathing structures in Muscineæ which envelop the clusters of archegonia and antheridia.

Peridium, the outer envelope investing the fructification in certain Fungi.

Perine, the outmost layer of sculpturing on the membrane of pollen-grains.

Perisperm, the tissue of the nucellus, in which, sometimes, food material is stored for the ultimate use of the embryo. It is external to the embryo-sac. In many old systematic books it is used for all food-material of seeds which is external to the embryo.

Peristome, the ring of teeth around the mouth of a Moss capsule.

Perithecium, the flask-shaped cavity in which asci are produced in certain Fungi.

Petal, a corolla-leaf.

Petaloid, -ine, like a petal.

Petiole, the stalk of a leaf.

"Petit grain", name for the ethereal oil yielded by the leaves of the Orange-tree.

Phænology, that branch of botanical investigation which deals with the recording, tabulation, and comparison of the times and seasons at which plants open their flowers and perform other periodic functions in various portions of the globe.

Phanerogamia, seed-bearing or flowering plants.

Phloem, soft bast; the soft outer portion of a vascular bundle, of which sieve-tubes are the most characteristic constituents.

Phrygana, an old term for a growth of stiff and prickly under-shrubs.

Phycocyanin, the blue pigment of the Cyanophyceæ or lowest Algae.

Phycophæin, the brown pigment of the Brown Algæ.

Phycoerythrin, the purple colouring-matter of Red Sea-weeds.

Phylloclade, a branch assuming form and function of a foliage-leaf: same as *cladode*.

Phyllode, a petiole assuming the form and function of a leaf-blade.

Phyllotaxis, leaf-arrangement; the arrangement or order of distribution of leaves on the stem.

Phylogeny, or **Phylogenesis**, the history of the genealogical development of an organized being; the race history of an animal or plant, as distinguished from *ontogeny*, the history of individual development.

Phylum, a main division of the vegetable kingdom.

Pileus, the cap-shaped receptacle of a Basidiomycetous Fungus; the umbrella-like part of a mushroom.

Pili fasciculati, tufted hairs.

Pili stellati, stellate hairs.

Pinnate, when leaflets are arranged on either side of a common rachis or petiole.

Pistil, the female organ of a flower, consisting of ovary (style) and stigma; if the carpels are apocarpous there are many pistils; if syncarpous, only one.

Pistillate, said of a plant or flower containing a pistil; most correctly, of one having no stamens.

Pitcher, a tubular or excavated leaf, usually containing a liquid; an ascidium.

Pith, the central cellular part of a stem or root.

Pits, thin places or depressions on cell-walls.

Placenta, the part of the carpel which bears the ovules; in Vascular Cryptogams, the portion of leaf-surface bearing the sporangia.

Plaited, folded; folded into plaits lengthwise; plicate.

Plant-formation, a term used to indicate the presence of two or more types of plant-community intermingled together, often in obvious strata. Cf. vol. ii. p. 896.

Plasmodium, in the Myxomycetes; a mass of naked multi-nucleate protoplasm exhibiting amœboid movements.

Pleomorphism, the occurrence of more than one independent form in the life-cycle of a species, especially in Fungi and Bacteria.

Pleurocarpous, used of Mosses in which the archegonia are borne, not at the tips of the main but of secondary shoots.

Plicate, of æstivation; folded lengthwise in plaits.

Plumule, the rudimentary shoot of an embryo.

Pod. See *Legume*.

Podium, a term for the torus or floral receptacle.

Polar nuclei, the two nuclei—one from each end of the embryo-sac of Angiosperms—which approach one another and fuse to form the definitive nucleus of the embryo-sac.

Pollarding, the act of removing the crown of a tree so as to induce it to throw out branches around the place of amputation.

Pollen, the mass of fecundating cells or grains contained in the anther.

Pollen-grain, one of the fecundating cells of the pollen; the microspore in flowering plants.

Pollen-sac, the sporangium in which the microspores or pollen-grains of flowering plants are developed.

Pollen-tube, the tubular outgrowth of a pollen-grain by means of which fertilization is achieved.

Pollinia, masses of coherent pollen-grains.

Polycarpellary, having or consisting of a number of carpels.

Polychotomous, branching repeatedly into equivalent portions.

Polyembryony, the production of more than a single embryo in an ovule.

Polyhedra, angular bodies which arise from the zoospores into which the zygote of Hydrodictyon breaks up. Ordinary Hydrodictyon-nets arise inside them.

Porogamic, used of flowering plants in which the pollen-tube effects an entrance to the ovule by the micropyle.

Porous, used of dehiscence of anthers, &c., by means of holes.

Prickle, a sharp-pointed process of the epidermis or cortex, but destitute of vascular tissue.

Primordial utricle, that portion of the cell-protoplasm which forms a bag in contact with the cell-wall. An old name which has persisted in the terminology.

Procumbent, lying along the ground.

Prolepsis, something of the nature of an anticipation. See vol. i. p. 8.

Pro-mycelium, the limited tubular growth arising from the chlamydospores in Hemibasidii and Uredineæ, from which conidia are abstricted.

Prostrate, lying flat on the ground.

Protandrous, Proterandrous, used of flowers when the anthers dehisce before the stigmas are receptive.

Proteid, a nitrogenous substance of complex constitution, generally of a viscid nature and rarely crystallizable. The proteids include albumin, globulin, peptone, &c.

Prothallus, -ium, the structure produced by the germination of the spore of Ferns, bearing sexual organs, and from which the young plant arises and derives nourishment for a time; also the homologue of this in flowering plants.

Protogynous, Proterogynous, used of flowers in which the stigmas are receptive before the pollen of the same flower is discharged.

Protonema, the filamentous growth of a Moss from which the leafy shoots arise by budding.

Protoplasm, the living and formative organic substance of plants and animals; living matter in its simplest form, serving as the basis of both animals and plants, and consisting of carbon, oxygen, hydrogen, and nitrogen, colourless, transparent or nearly so, and somewhat viscid in consistence.

Protoplast, the protoplasmic cell-body; a simple one-celled organism.

Pseudo-hermaphrodite flowers are such as have been functionally unisexual by the suppressing of either stamens or carpels.

Pseudomorph, a term borrowed from mineralogy; an unusual or altered form. Cf. vol. i. p. 185.

Pulverulent, powdery.

Pulvinate, cushion-like.

Pulvinus, the enlargement of a petiole or leaf-stalk at its point of insertion on the stem, or of a secondary petiole at its point of insertion on the leaf-rachis.

Pycnidium, in Fungi; a receptacle or cavity of varying form, in which conidia (pycno-conidia) are produced: especially in Ascomycetes.

Pyrenoids, refractive bodies imbedded in the chlorophyll of many Green Algæ.

Race, a variety or form not distinguished by characters important enough to rank as a species, but reproduced by seed and transmitting its characters to the offspring; also loosely used for a group of allied individuals without regard to rank.

Racemus, Raceme, an indefinite or centripetal inflorescence with pedicellate flowers.

Rachis, the axis of a compound leaf, or of a spike or other indefinite inflorescence.

Radical, belonging to or arising from a root, or from a root-like portion of the stem below the ground.

Radices adligantes, clinging roots.

Radices columnares, columnar roots.

Radices fulcrantes, stilt-like roots.

Radices parietiformes, or tabular roots. See vol. i. p. 754.

Radices tuberosæ, or tuberous roots; roots beset with tuber-like enlargements.

Radicle, the root of an embryo; usually not separable from the hypocotyl.

Radix, the root.

Raphe, that part of the stalk of an anatropous ovule which is fused with the body of the ovule; in Diatoms, the median line on the frustule, possibly a slit.

Receptacle, of a flower; the abbreviated or flattened axis upon which the various floral members are inserted.

Reniform, kidney-shaped.

Replum, the framework, or frame-like placenta, which remains in Cruciferous and other fruits after the valves have fallen away.

Resilient, springing back, rebounding: used of fruit-stalks, stamens, &c.

Resin-duct, an intercellular passage into which resin is secreted and where it is stored.

Respiration, the term applied to the absorption by a plant of free oxygen from, and evolution of carbon dioxide into the air. It is the outward sign of a destructive oxidative process going on within the plant, by means of which latent energy is rendered available.

Revert, Reversion, a sudden return or breaking back to an ancestral form.

Revolver-flowers. See vol. ii. p. 249.

Rhizoids, the hair-like filaments of Mosses and Liverworts, which perform the functions of roots.

Rhizome, an underground (or prostrate) stem of root-like appearance from which roots and herbaceous stems arise.

Rhizomorph, name given to the curious vegetative phase of Agaricus melleus, which resembles a root.

Rhizophore, a leafless branch of peculiar construction which, in Selaginella, arises at the place where ordinary branching takes place, and bears roots at its free end.

Rhizotomoi, a guild of herbalists in ancient Greece.

Ring, Annual, the zone of wood formed from the cambium in the course of one season in a Conifer or Dicotyledon.

Ringent, gaping, as the mouth of a bilabiate corolla.

Ringing, the act of removing from a branch or trunk a circular zone of bark right down to the wood.

Root-cap, the cellular cushion produced at the apex or tip of a root.

Root-stock. Same as *rhizome*.

Rostellum, the morphological apex of the gynœceum of an Orchid; usually a beak forming the boundary between the stamen and stigma in Orchids.

Rosulate, collected in form of a rosette.

Rotate, wheel-shaped; circular and horizontally spreading.

Runner, a prostrate filiform branch which is disposed to root at the end or elsewhere.

Samara, an indehiscent winged fruit, as the *key* of the Ash or Maple.

Saprophyte, a plant which grows on dead and decaying organic matter.

Scabrous, rough to the touch.

Scape, or **Scapus**, a peduncle rising from the ground.

Scarious, thin, dry, and membranaceous, and not green.

Schizocarp, a polycarpellary fruit which breaks into 1-seeded portions.

Sclerotic-cell, a hard, thick-walled cell, often of irregular form; sclerotic cells may be united together into layers, or isolated in soft parenchyma.

Sclerotium, in Fungi a tuber-like mass of hyphæ, which, after remaining dormant for a while, ultimately sprouts, producing fructifications. In the Myxomycetes it is the resting-stage of the plasmodium.

Scorpioid cyme, a definite inflorescence rolled up towards one side like a crook: common in Boraginaceæ.

Scutellum, the sucker or cotyledon of a Grass embryo.

Scutiform, having the form of a shield.

Seed, the fertilized and matured ovule.

Seed-coat, the integument of the seed, formed from the investment or investments of the ovule.

Seedling, a young plant raised from a seed.

Semifrutex, or **Semi-shrub**, a shrub the shoots of which become woody at the base only, this portion alone being perennial.

Sepal, a leaf-member of the calyx.

Sepaloid, resembling a sepal.

Separation-layer. See *Absciss-layer*.

Septum, a partition; a thin wall separating compartments.

Sericeus, silky; clothed with soft straight hairs.

Serrate, of leaf-margins; beset with teeth pointing towards the apex.

Sessile, destitute of stalk, petiole, or pedicel.

Seta, a bristle; the stalk of the spore-capsule in a Moss or Liverwort.

Shoot, that portion of the plant which is differentiated into stem and leaves and bears the reproductive organs.

Sieve-cells, cells which have pores in their walls causing a sieve-like appearance; sieve-tubes.

Sieve-plates, areas in the walls of sieve-cells or sieve-tubes perforated by pores.

Sieve-tube, an articulated tube whose contiguous elements communicate by means of open pores aggregated together upon sieve-plates. The sieve-tube is the characteristic element of the phloem.

Siliqua, the fruit of a Cruciferous plant, a longish pod or seed-vessel. Cf. vol. ii. p. 432.

Sinistrorse, used of twining stems which turn from north through west to south, &c.: the opposite of *dextrorse*.

Sinuous, Sinuate, used of a leaf-margin which is strongly indented in a wavy manner.

Sling-fruit, a general term given to any fruit which, in virtue of the possession of contractile tissues, throws its seeds to a distance, or is itself so thrown.

Soboles, a thin creeping stem, often subterranean.

Soredium, the 'brood-body' or 'brood-bud' of a Lichen, consisting of a few algal cells wrapt round with a weft of fungal hyphæ.

Sorus, a cluster of sporangia, such as those of Ferns.

Spadiciform, like a spadix.

Spadix, a fleshy spike.

Spathe, a large bract-like sheath inclosing an inflorescence.

Spatulate, like a spatula, oblong with the lower end attenuated.

Species. Under this term may be included all individuals which possess in common such a number of characters that they may be regarded as being descended from a common ancestral form.

Spermatium, a male sexual cell which becomes free, but is unprovided with special organs of locomotion.

Spermatoplasm, the protoplasm of the male sexual cell.

Spermatoplast, a male sexual cell.

Spermatozoid, a free-swimming male sexual cell provided with cilia as organs of locomotion.

Spike, an indefinite inflorescence with flowers sessile on an elongated axis.

Spine, a sharp-pointed body possessing vascular tissue, commonly a branch or some portion of a leaf.

Sporangiole, in the Fungi; a small sporangium, usually containing few spores, and larger many-spored sporangia being also present.

Sporangiophore, that which bears sporangia; a scale bearing sporangia in Equisetum.

Sporangium, a sac within which spores are developed.

Spore, a reproductive cell which becomes free, and is capable of developing into a new individual.

Sporidium, a spore abjointed from a pro-mycelium.

Sporocarp, a fructification, often the result of a sexual act, in which spores are produced, as in Red Sea-weeds and Fungi. Also used of the sporangial receptacles of the Hydropteridæ.

Sporogonium, in Mosses; the so-called 'moss-fruit' with its appendages, consisting mainly of the capsule and seta or stalk.

Sporophyte, that stage in the life-cycle of a plant which bears the spores. Cf. *Oophyte*.

Spur, an excavated slender continuation of some portion of a flower, usually containing nectar.

Squamiform, scale-like.

Squamigerous, furnished with scales.

Stamen, the male organ in a flower, which produces pollen. It consists of the filament or stalk, and the anther, in which the pollen is contained and which is supported by the filament. The stamens collectively form the androecium.

Staminate, having stamens.

Staminiferous, bearing stamens.

Staminode, a sterile stamen.

Standard, in papilionaceous flowers, is the unpaired, posterior petal.

Sterigma, the tube or stalk-like branch from which conidia are abstricted.

Stigma, that portion of the pistil which receives the pollen.

Stipules, paired foliaceous appendages of the leaf-base.

Stirps cirrhosa, a tendril-bearing stem.

Stirps clathrans, a lattice-forming stem. See vol. i. p. 678.

Stirps fluctuans, a floating stem.

Stirps humifusa, a prostrate stem.

Stirps palaris, a standard-stem, *i.e.* an erect, unbranched stem.

Stirps plectens, a weaving stem. See vol. i. p. 671.

Stirps radicans, a stem which climbs by means of roots.

Stirps volubilis, a twining stem.

Stock, the parent forms from which a hybrid is derived.

Stolon, or **Stolo**, a procumbent stem which bears buds which take root; the buds are more frequent and the internodes shorter than in the runner.

Stoma, an intercellular space or pore in the epidermis which, bounded by adjustible guard-cells, forms the means of communication between the lacunæ of the plant and the outside air.

Stratification, the layering of cell-walls or starch-grains.

Stroma-starch, in certain Algæ (*e.g.* Hydrodictyon), the fine-grained starch deposited throughout the chlorophyll-body, which plays a different part in the economy of the plant from that deposited around the pyrenoid. Cf. vol. ii. p. 640.

Style, the usually attenuated prolongation of an ovary upon which the stigma is borne.

Sub-capitulum, a secondary capitulum.

Suberin, a corky substance; the substance or group of substances present in cuticularized or corky cell-walls.

Subex, a stem bearing scale-leaves.

Succulent, fleshy, pulpy.

Sucker. See *Surculus*.

Suffrutex, an under-shrub; a woody plant of quite humble growth.

Suffruticose, somewhat shrubby.

Surculus, or **Sucker**, a shoot arising from a subterranean base.

Suspensor, in Flowering Plants and in Selaginella; the filament of cells at the lower extremity of which the embryo arises.

Suture, a line of union, very frequently the line along which dehiscence also takes place.

Swarm, a social aggregate of simple organisms which live together but are not attached to any substratum.

Swarm-spore, a motile, ciliated, asexual reproductive cell destitute of a cell-membrane.

Switch-plant, a plant with reduced or wanting leaves, the shoots of which are green and subserve the functions of leaves.

Symbiosis, the association of two organisms which live together in intimate connection, both contributing to their mutual welfare.

Syncarpous, said when the carpels of a gynœceum are united.

Synconium, the fleshy excavated inflorescence of a Fig.

Synergidæ, two naked cells situated at the micropylar end of the embryo-sac, and assisting in the passage of the male cell to the egg in porogamic fertilization.

Syngenesia, the 19th class of the Linnean system.

Syngenesious, having coherent anthers.

Systole, the rhythmic contraction of a contractile vacuole.

Tagmata, aggregates of micellæ.

Tapetal cells, the layer of cells immediately external to the archesporium, and becoming latterly disorganized with the maturing of the spores (or pollen-grains).

Teleutospore, in Uredineæ, a resting-spore which on germinating gives rise to a pro-mycelium or basidium.

Tenaculum, the clasping, rosette-like clamps of Struvea, by means of which independent branches are held together.

Tendril, a filamentous branched or unbranched organ, usually sensitive to contact, by means of which a plant climbs.

Tentacle, an irritable hair or emergence on a leaf, as in Dionæa, Drosera, &c.

Terete, round, *i.e.* circular in transverse section.

Ternary hybrid, the plant resulting from crossing a hybrid with a species different from either of its parent forms.

Ternate, used of compound leaves with three leaflets, one terminal and two lateral.

Testa, the integument of a seed, often arising from the outer of the two ovular coats.

Tetrad, a group of four cells (*e.g.* spores, pollen-grains), usually arranged in the four corners of a 4-sided pyramid (tetrahedon).

Tetradynamia, the 15th class of the Linnean system.

Tetradynamous, used of stamens when there are six, of which four are longer than the other two—as in Cruciferæ.

Tetraspores, the asexual spores of Red Sea-weeds, usually aggregated in clusters of four.

Thalamus, the floral receptacle.

Thallidium, a vegetative reproductive body, especially amongst Thallophytes and Muscineæ.

Thallus, a vegetative body without differentiation into stem and leaf.

Thermal constants of vegetation. See vol. i. p. 557.

Tissue, a continuous aggregate of cells having a common origin.

Tomentose, felty or invested in tomentum.

Tomentum, dense matted investment of woolly hairs.

Torus, (1) the floral receptacle; (2) the thickening on the pit-closing membrane of a bordered pit.

Trabeculæ, folds or ridges projecting into a cell from the wall; the term also given to strings of filamentous cells bridging intercellular spaces.

Tracheids, elongated, pointed, and more or less lignified cells occurring in wood.

Transpiration, the act of exhaling aqueous vapour from foliage or other portions of plants.

Trichoblasts, fusiform hard-walled cells. Not a good term.

Trichogyne, the filamentous portion of the female sexual apparatus of a Red Sea-weed, which receives the spermatia.

Trichome, a hair-like or similar outgrowth of the epidermis.

Truncate, appearing as if cut short at the tip.

Trunk, a main stem.

Tuber, a subterranean, somewhat fleshy shoot.

Tubercle, a small excrescence.

Tumescent, becoming enlarged, distended.

Turgescence, Turgidity, the state of tension set up within a cell owing to the pressure of the osmotic cell-contents upon the elastic cell-wall.

Turion, a subterranean budding shoot, especially in perennials.

Umbel, an inflorescence in which a cluster of flower-stalks arises all from the same point.

Unguiculate, narrowed at the base into a claw: used of petals.

Urceolate, hollow and contracted at or below the mouth like an urn.

Uredospore. See vol. ii. p. 686.

Utricle, an archaic term for a parenchyma-cell.

Vacuole, a cavity in the protoplasm containing cell-sap.

Vagina, the sheathing portion of a leaf-base.

Valvate, having valves; opening by valves; also, used of the arrangement of the parts of a flower-bud when they just meet but do not overlap. Cf. vol. ii. p. 210.

Valve, (1) in flowering plants, the pieces into which a capsule breaks are termed valves; also the movable flaps in the dehiscence of anthers; (2) in Diatoms, the valves are the halves of the silicified membrane or shell, also called *frustules*.

Variegation, a term employed to designate the disposition of two or more colours in the petals, leaves, and other parts of plants.

Vascular bundle, a continuous strand of vascular tissue, consisting either of xylem or phloem, or of both. Not infrequently sclerenchymatous elements are associated with the bundle, when it is termed a fibro-vascular bundle.

Vascular elements, cells or vessels whose main function is the distribution of water or formed food-substances. The chief of them are the vessels and tracheids of the wood, and the sieve-tubes of the phloem.

Velum, in Isoëtes; the indusium-like membrane which covers the sporangium.

Velum partiale, in Hymenomycetes; the veil stretching from the stipe to the edge of the pileus. It often remains as the annulus.

Velum universale, in Hymenomycetes; the membranous wrapper inclosing the whole fructification.

Venation, the arrangement or pattern of the vascular bundles in a leaf.

Ventral canal-cell, the small cell which is cut off from the central cell of an archegonium immediately below the neck.

Ventricose, unequally swollen.

Vernation, the arrangement of the parts in the bud, especially a vegetative bud.

Verrucose, covered with warts.

Versatile, turning freely on its support.

Verticillate, arranged in a whorl.

Vessel, a tube consisting of cells which have become confluent by the partial or complete absorption of the intervening walls. They are common in the wood of Angiosperms.

Viviparous, term applied to plants the seeds of which germinate whilst still on the parent plant.

Volva, same as *velum universale*.

Whorl, a series of appendages arranged in a circle around an axis.

Witches' Broom, a form of gall found on the Silver Fir and other Conifers; sometimes applied to the bird's-nest-like hypertrophies on the Birch, &c.

Wood, the hard, lignified portion of the vascular tissue otherwise known as the *xylem*. It contains tracheids, woody fibres, and wood parenchyma, though not all of these are necessarily found in the wood of any given plant.

Xenogamy, pollination between flowers growing on different individuals of the same species.

Xylem, the woody portion of vascular tissue. See *Wood*.

Zoogloea, a solid gelatinous colony of Bacterial organisms.

Zygomorphic, applied to flowers which are symmetrical about one plane only, or can be cut into similar halves in only one plane.

Zygospore, a spore formed by the union of two gametes.

Zygote, a general term for the product of fusion of two gametes.

Zygozoospore, the motile stage of a zygote, the product of fusion of two motile gametes.

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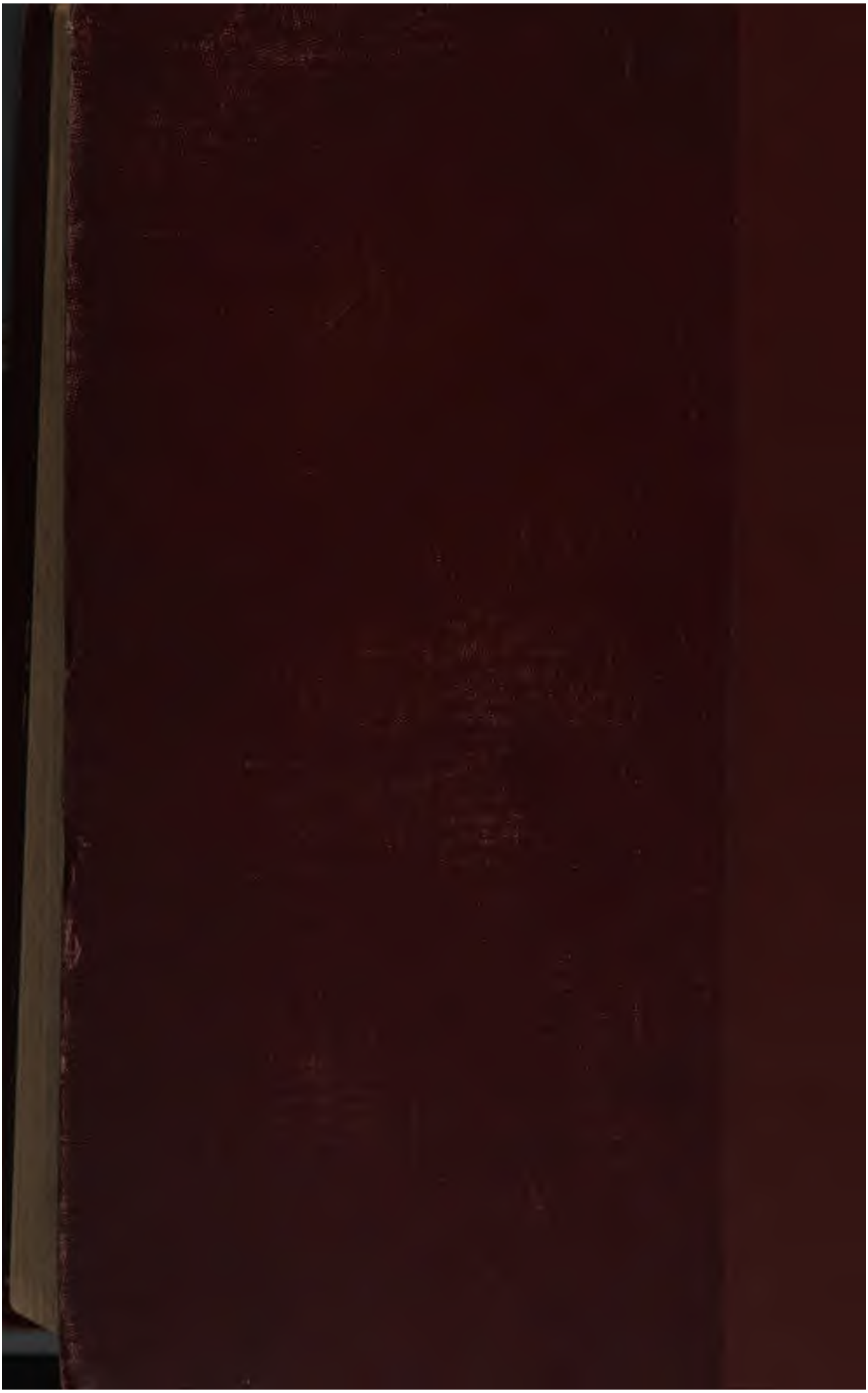
— of Spirogyra, ii. 658.
— of Volvox globator, ii. 635.
Zygotes of Ulothrix zonata, ii. 648.
Zygozoospore, formation, ii. 632.
Zygozoospores, of Chlorochytrium, ii. 637.
— of Phyllobium, ii. 638.
— of Stephanosphæra, &c., ii. 632.

END OF VOL. II.